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CLASSIFICATION OF EUROPEAN FORESTS

Syntaxonomy of the class *Alnetea glutinosae* in Ukraine: a critical revision

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Abstract

Aims: (a) To revise the previous classification systems for the *Alnetea glutinosae* vegetation in Ukraine using a representative dataset; (b) to define the vegetation types at the association level and outline their geographical distribution and species composition; (c) to describe the relationships between the defined associations and the main environmental factors. **Study area**: Ukraine. **Methods**: 5818 vegetation plots of floodplain forests, alder carr, and birch forests were collected in the field and digitized from the literature. We used PC-ORD beta-flexible clustering (beta = –0.3, Bray-Curtis dissimilarity, log-transformed percentage abundances) to distinguish the vegetation types. We plotted the classification results using an NMDS ordination diagram to visualize the similarity patterns among the vegetation types. **Results**. We distinguished six associations within three alliances: mesotrophic regularly flooded alder carr (*Thelypterido palustris-Alnetum glutinosae*, *Carici elongatae-Alnetum glutinosae*, *Carici acutiformis-Alnetum glutinosae*), basiphilous birch forests on mesotrophic mires (*Salici pentandrae-Betuletum pubescentis*) and acidophilous wet birch forests (*Thelypterido palustris-Betuletum pubescentis*, *Eriophoro vaginati-Betuletum pubescentis*). Using NMDS-ordination and Ellenberg-type indicator values we demonstrated that the main gradients for vegetation differentiation are the soil moisture and soil reaction, nutrients, and light availability. **Conclusions**: Using our comprehensive data set, we critically revised the previous concept and syntaxonomic structure of the class *Alnetea glutinosae* in Ukraine. We distinguished six phytosociological associations and highlighted the main environmental drivers determining vegetation differentiation and variability. Our study also provides an overview of the current distribution for each association of the *Alnetea glutinosae* in Ukraine.

Taxonomic reference: Euro+Med (2006-) for vascular plants, Hodgetts et al. (2020) for bryophytes.

Syntaxonomic reference: Higher syntaxa follow Mucina et al. (2016).

Abbreviations: db-RDA = distance-based redundancy analysis; EIVs = Ellenberg indicator values; EVC = EuroVeg-Checklist, GIVD = Global index of vegetation plot databases, ICPN = International code of phytosociological nomenclature (Theurillat et al. 2021); NMDS = Non-metric multidimensional scaling; NNP = National nature park.

Keywords

alder carr, *Alnion glutinosae*, *Betulion pubescentis*, birch forest, classification, environmental gradients, ordination, forest vegetation

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Introduction

The class *Alnetea glutinosae* includes swamp forests on periodically flooded minerotrophic and organic soils occurring in shallow depressions in river floodplains and terraces, old river channels, swamp and mire margins, banks of lakes, water reservoirs, ponds and other waterlogged low-lying areas with high stagnant groundwater table and relatively stable water regime (Douda 2013; Slezák et al. 2014). This vegetation has a broad Eurosiberian distribution across lowlands and uplands (Douda et al. 2016; Preislerová et al. 2022) reaching the subalpine belt in mountains (Sburlino et al. 2011; Slezák et al. 2013). The occurrence of the *Alnetea glutinosae* has also been documented in southwestern Asia (Gholizadeh et al. 2020) and North Africa (Amigo et al. 2004). These azonal plant communities develop under the strong influence of the changing hydrological regime (Solińska-Górnicka 1987; Oberdorfer 1992) and are less dependent on the biotic, climatic, and soil conditions that influence zonal vegetation (Koljanin et al. 2023). The variation of floristic composition across this vegetation with changing climate is not as evident as for surrounding zonal vegetation types, including forest vegetation (Döring-Mederake 1990; Rodríguez-González et al. 2014).

The vegetation of the *Alnetea glutinosae* usually consists of monospecific forest stands of black alder (*Alnus glutinosa*) and/or downy birch (*Betula pubescens*) with a specific combination of plants in the herb layer. This complexity in the floristic composition is a result of variation in the soil moisture gradient within the swamp forests. Alternation of the waterlogged hollows and drier hummocks, which is reflected in the microtopography of the habitat relief (Slezák et al. 2014), promotes the formation of a herb layer with a combination of wetland reeds, sedges, herbs, ferns, grassland species, ruderal plants, some aquatic and amphibious plants. Some *Alnetea glutinosae* plant communities are also characterized by a well-developed moss layer consisting of species with different ecological affinities (Hrivnák et al. 2021). Besides the local environmental variables, reflected in physical and chemical soil characteristics (Härdtle et al. 2003; Slezák et al. 2017; Serafin et al. 2022) and peculiarities of the hydrological regime (Kazda 1995; Pielech and Malicki 2018), the species composition of this vegetation is also driven by a set of regional factors (e.g. landscape configuration, elevation, local climatic parameters) (Douda 2010; Hrivnák et al. 2021). The historical processes, such as postglacial migration of plants can also influence species pool and affect the compositional variability of the swamp forests (Brown 1988; Pokorný et al. 2000; Barthelmes et al. 2010; Douda et al. 2018; Hrivnák et al. 2020).

Encompassing the physical environment and biological communities of the inland–freshwater interface, swamp forests are highly diverse ecosystems compared to surrounding areas (Rodríguez-González et al. 2022; Koljanin et al. 2023). They represent important biodiversity hotspots (Prieditis 1999; Ward et al. 1999; Sabo et al. 2005; Pilate 2009). These ecosystems provide crucial ecosystem services related to biodiversity conservation, supporting hydroregime across landscapes, prevention of erosion processes, nutrient retention, carbon fixation, etc. (Hanna et al. 2018; Riis et al. 2020; Stammel et al. 2020). The significant ecological role of swamp forests, particularly birch forests, and their vulnerability to human impact was recognized by the Habitat Directive (92/43/EEC) (European Council 1992), which, under the code 91D0, included them in the list of Habitats of Community Interest, and the European Red List of Habitats under the category "Vulnerable" (Janssen et al. 2016). These habitats are also on the priority list of the EU's Biodiversity Strategy for 2030 (European Commission 2020).

Unlike other types of forest ecosystems, which are significantly impacted by forestry and clearance, the major threat for the swamp forests are changes in the hydrological regime of landscapes connected with canalization and water deviation, lack of flooding, rivers modifications, water abstractions from surface or groundwater, pollution and eutrophication of surface water (Czerepko et al. 2005; Janssen et al. 2016; Rohde et al. 2021). No less essential is the impact of climate changes, habitat fragmentation, losses of habitat connectivity, intensive agriculture, and urbanization. Over the past years, swamp forests have been increasingly affected by *Phytophthora* infections (Bregant et al. 2020, 2023; Nave et al. 2021; Corcobado et al. 2023; Tkaczyk et al. 2023; Gomes Marques et al. 2024), and faced growing global threats from alien plant invasions (Richardson et al. 2007; Patalauskaitė 2010; Pyšek et al. 2010; Wagner et al. 2017; Langmaier and Lapin 2020; Viciani et al. 2020; IUCN 2021; Grzędzicka 2023). The swamp forests, particularly their vegetation cover, are changing in species composition, physiognomic structure, and function as a result of the direct or indirect effects of all the factors listed. In this aspect, syntaxonomic studies providing clearly defined vegetation units are the key baseline for nature conservation planning, management, and monitoring (Rodwell et al. 2018).

Syntaxonomic research of the class *Alnetea glutinosae* across the European continent has been presented in numerous local (Jurko and Májovský 1956; Pancer-Kotejowa 1973; Kliment and Watzka 2000; Šomšák 2000; Kollár et al. 2005; Gargano et al. 2007; Koczur 2011; Slezák et al. 2011; Hrivnák et al. 2013; Dubyna and Dziuba 2014; Poldini et al. 2020) and regional (Czerwiński 1972; Döring-Mederake 1990; Prieditis 1997; Amigo et al. 2004; Biurrun et al. 2014; Gennai et al. 2021; Koljanin et al. 2023) studies. National overviews developed to the different levels of the syntaxonomic hierarchy have been published for most European countries (Prieditis 1993; Rivas-Martínez et al. 2001; Bardat et al. 2004; Lawesson 2004; Franz and Willner 2007; Sanda et al. 2008; Paal et al. 2008; Tzonev et al. 2009; Sburlino et al. 2011; Costa et al. 2012; Borhidi et al. 2012; Šilc and Čarni 2012; Matuszkiewicz 2012; Douda 2013; Skvorc et al. 2017; Dubyna et al. 2019; Hrivnák et al. 2021). The first European synthesis of

the class *Alnetea glutinosae* was presented by Bodeux (1955). The results of long-term research on the class at the continental scale were summarized by Mucina et al. (2016), who presented the "syntaxonomic backbone" of the hierarchical system of the *Alnetea glutinosae* at the levels of orders and alliances, and by Douda et al. (2016), who developed a syntaxonomic summary and formalized classification at the level of associations.

Phytosociological research on the class *Alnetea glutinosae* has a long tradition in Ukraine. The first detailed vegetation survey of the swamp forests at the national scale was performed using the dominant approach (Bradis 1971). The phytosociological studies of the *Alnetea glutinosae* using the Braun-Blanquet approach were started by V. Solomakha (1995), who mentioned one association of the class in the first synthesis of the vegetation of Ukraine. With further active implementation of this methodology in Ukraine, many local phytosociological studies dealing with *Alnetea glutinosae* were conducted (Bairak 1997; Vorobyov et al. 1997; Grygora et al. 2005; Onyshchenko 2006; Soroka 2008; Chorna 2013; Panchenko 2013; Dubyna and Dziuba 2014; Solomakha et al. 2015; Kozyr et al. 2023). A national overview of this vegetation at the association level was published by Solomakha (2008) and the author combined alder and willow carrs within the class *Alnetea glutinosae*. In this syntaxonomic synopsis, Solomakha (2008) considered 10 of the 14 phytosociological associations relevant to alder carr. He also classified two associations with *Betula pubescens* within a separate alliance of the class *Vaccinio-Piceetea*. Dubyna et al. (2019) summarized all the known information in the current edition of the "Prodrome of the Vegetation of Ukraine". According to Dubyna et al. (2019) 10 vegetation associations representing alder carr and one vegetation association covering birch forests on mires occur in Ukraine. However, all of the local and national reviews cited were mostly based on an analysis of literature sources, without strictly following nomenclature rules (Weber et al. 2000; Theurillat et al. 2021) and without using modern data analysis techniques and tools. Some syntaxonomic issues were decided based on the analysis of local datasets, and therefore, unfortunately, have only local validity.

Modern international vegetation-plot databases have opened up new research opportunities (Dengler et al. 2011; Chytrý et al. 2016; Bruelheide et al. 2019). Together with advances in vegetation classification methodology (De Cáceres et al. 2015), they provide unique opportunities to process vegetation data on a national scale and develop comprehensive overviews for different vegetation and habitat types.

In this study, we gathered vegetation plots for the class *Alnetea glutinosae* across all of Ukraine with the aims of (a) revising previous classification systems using a representative dataset; (b) defining vegetation types at the association level and outlining their geographical distribution and species composition; (c) describing the relationships of defined vegetation associations to the main environmental factors.

Study area

Our research covered the whole territory of Ukraine which stretches in a west-east direction for 1316 km and extends for 893 km in a north-south direction. The study area encompasses an area of 603,700 km^2. Ukraine is divided into three physio-geographic zones (forest, forest-steppe, and steppe), which are distinguished by the types of landscapes, their geological, geomorphological structure, and climatic features (Marynych et al. 2003). The relief of the territory of Ukraine is represented by lowlands (70% of the territory), uplands (25%), and mountains (5%) (Marynych and Shyshchenko 2005). Most of the lowlands are dominated by glacial, fluvioglacial, and alluvial geological deposits. The uplands are covered by a thick loess stratum that overlies various geological layers cut by gullies and ravines (Paliyenko 2005). Most of Ukraine is influenced by a temperate climate with mild winters and dry hot summers. The average temperature in January varies in a submeridional direction, ranging from –3° C in the far west to 0° on the southern coast of Crimea. The average temperature in July ranges from 19° to 23°. Annual precipitation is unevenly distributed across Ukraine, ranging from 700 mm in the northwest to 550 mm in the forest-steppe zone, 450 mm in the steppe zone, and 300 mm on the Black Sea–Azov coast. Annual precipitation has significant inter-annual variability resulting in both very wet and very dry years (Rudenko 2007). The average density of the river network in Ukraine is 0.25 km/km^2. Most of the large river valleys are wide and terraced with gentle slopes. Some rivers' valleys across the forest zone are not incised, wide, and very swampy (Vyshnevskyi and Kosovets 2003). Soil cover varies in different physic-geographical zones. In the forest zone, in conditions of high precipitation and shallow standing groundwater, sod-podzolic soils formed on sandy and sandy loam alluvial, glacial, and moraine deposits predominate. In the forest-steppe zone, where forest and meadow-steppe areas alternate, the prevalent soil types are grey forest soils on carbonate rocks and typical or podzolic chornozems on light loesses. The steppe zone is an area with a diverse soil mosaic. The northern part is occupied by typical chornozems with medium- and low-humus content. The middle zone is covered by southern chornozems. Chestnut soils, in combination with solonetz and solonchaks, occupy the south of the Black Sea lowlands and the north of Crimea (Rudenko 2007). According to the world's terrestrial biomes classification (Loidi et al. 2022, 2023) Ukraine is located within two biomes: the biome of the temperate deciduous forest and the biome of the steppe.

Due to the azonal character of the target vegetation, the studied localities were distributed throughout Ukraine, with the predominant distribution within the forest and forest-steppe zone (Figure 1). In the forest-steppe zone, the main area of the swamp forests are concentrated in the floodplains of rivers, much less frequently they are situated on the low-lying localities of the river terraces. In the steppe zone, our research was conducted in the estuary of the Dnipro River – the main locality for this vegetation within southern Ukraine.

Figure 1. Study area and distribution of the vegetation plots used for the analysis (brown dots, n = 933).

Methods

Data sampling and data filtering

The data for this study were 5818 vegetation plots (phytosociological relevés) of floodplain forests, alder carr, and birch forests sampled by the authors during the period 2014–2022, supplemented by data from local literature sources. The phytosociological relevés were sampled using the Braun-Blanquet approach (Braun-Blanquet 1964) on plot sizes ranging from 25 to 1600 m^2. All vegetation plots are stored in the "Database of the Floodplain Forests of Ukraine" (managed by L. Borsukevych) and "Ukrainian Wetland Database" (registered in GIVD with the code EU–UA–012) using Turboveg database software (Hennekens and Schaminée 2001).

We have accepted the phytosociological concept and structure of the class *Alnetea glutinosae* according to EVC (Mucina et al. 2016), and therefore for the analysis we selected only vegetation plots with dominance (more than 25% cover) of *Alnus glutinosa* and *Betula pubescens*. The selection resulted in a total of 2153 vegetation plots that were sampled from 1952 to 2022 and: (i) were georeferenced or did not contain geographical coordinates; (ii) were of a plot size 40–1600 m^2. Since the selected vegetation plots were quite heterogeneous in quality, we performed data filtering before further analysis and producing the synoptic tables for the syntaxa. To minimize the potential impact of different plot sizes on constancy we only retained plots with a plot size of 100–400 m^2 (Chytrý and Otýpková 2003; Dengler et al. 2009). Then we eliminated plots with missing geographical coordinates, except for those plots where it was possible to add coordinates according to the description of localities in the sources. The final dataset, we used to develop the classification and ecological analysis of the *Alnetea glutinosae*, totaled 1826 plots. The complete list of the data sources for the final dataset used in this study can be found in Suppl. material 1.

All vegetation layers were combined into one. All records of vascular plant species and bryophytes that were not identified to the species level (respectively, 4 and 10% of the total taxa number) were removed from the final data matrix. Species taxonomy and nomenclature were standardized according to the Euro+Med (2024). To reduce taxonomic bias, we used the concept of broadly defined taxa and merged some species into aggregates (Suppl. material 2).

Data analysis

To build the classification we processed data in Juice 7.1 (Tichý 2002). We performed unsupervised classification using agglomerative clustering with the PC-ORD 5.0 (Grandin 2006). We used two-step beta flexible clustering (β = −0.3) with the Bray-Curtis index as a dissimilarity measure and square-root data transformation. The optimal number of clusters was selected using the OptimClass1 method (Tichý et al. 2010) considering the measure of classification crispness (Botta-Dukát et al. 2005). The first run of the numerical classification resulted in the separation of alder carr and birch swamps from other forests dominated by *Alnus glutinosa*. The latter (893 plots) were excluded and did not form part of this study. The remaining 933 plots were analysed with the same numerical classification settings as in the previous step. The OptimClass1 curve suggested the first peak at the level of 7 clusters, and we considered this number of clusters as the optimal partition to indicate the variability of the target vegetation in the study area. To confirm our syntaxonomic interpretation of the defined vegetation units, we added the original diagnosis of the associations (Schwickerath 1933; Scamoni 1935; Klika 1939–1940;

Soó 1955; Passarge and Hofmann 1968; Czerwiński 1972) we considered and reanalyzed the dataset.

We calculated diagnostic, constant, and dominant species for each association. We determined diagnostic species based on the concept of the fidelity, using the phi coefficient (Chytrý et al. 2002). Diagnostic species were defined as those for which the phi coefficient was ≥0.25. The significance of fidelity was tested using Fisher's exact test ($P < 0.001$). Only species with a frequency ≥25% were considered constant. Dominant species were defined as those occurring with a cover value >25% in at least 10% of plots. Since bryophyte records were not available for every plot in our dataset, we calculated the fidelity and frequency of bryophytes using only a subset of vegetation plots with bryophyte records, including plots with the explicit indication of the absence of a moss layer. In total, 678 plots were included in this subset, which was used both for the analysis and for the creation of synoptic tables for the species within the moss layer. This methodological approach followed those applied in recent syntaxonomic revisions of this and similar vegetation types (Douda 2013; Slezák et al. 2014; Douda et al. 2016; Hrivnák et al. 2021). All diagnostic species are listed by decreasing fidelity in the description of associations. Highly diagnostic species are presented in bold. All constant and dominant species are provided in Appendix 1. Diagnostic species for the higher syntaxa (alliances) are taken from the literature (Dengler et al. 2004; Douda 2013; Douda et al. 2016; Dubyna et al. 2019; Hrivnák et al. 2021).

We visualized the variation in plant species composition among defined associations using a NMDS ordination plot with square-root transformation of species percentage covers and Bray-Curtis dissimilarity measure. To compare the environmental affinity of associations, we used average unweighted EIVs (Tichý et al. 2023). To test for the significance of each ecological parameter we ran db-RDA with the same cover transformation and dissimilarity measure as in NMDS. We performed a modified permutation test for ANOVA (Zelený and Schaffers 2012; Zelený 2018) using function *summary.aov.iv* to check if there were significant differences among the vegetation associations for each significant environmental variable. Prior to performing this analysis, we assessed the data for potential violations of ANOVA assumptions. Normality was evaluated using the Shapiro-Wilk test, while homogeneity of variances was examined using Bartlett's test. The pairwise comparison Tukey's test between associations was employed to identify significantly different pairs. The results of pairwise comparisons are indicated using the Compact Letter Display method, where different letters indicate a statistically significant difference of the test, with $p < 0.05$.

We performed analysis in R 4.3.2 (R Core Team 2023) using the *vegan* 2.6-4 library (Oksanen et al. 2019 and visualized using the *ggplot2* package (Wickham 2016). Distribution maps were created using QGIS 3.34 (QGIS Development Team 2021).

We used EVC (Mucina et al. 2016) as the primary reference for the definitions and syntaxonomic nomenclature of the alliances and orders. Names of the associations were revised according to the 4th edition of the ICPN (Theurillat et al. 2021).

Results

Cluster analysis

The first cluster analysis run resulted in 15 clusters of vegetation plots and allowed us to split birch forests and alder carr from riparian alder vegetation. Since riparian alder vegetation was not the focus of this study we excluded these vegetation plots from further data processing. The results of the first step of the analysis, clusters interpretation with the lists of diagnostic, constant, and dominant species, are given in Suppl. material 3. In the second step of our analysis, we accepted a division into seven clusters (Figure 2). We assigned each cluster to a phytosociological association. The only exceptions were clusters 2–3, which we combined based on our expert judgment.

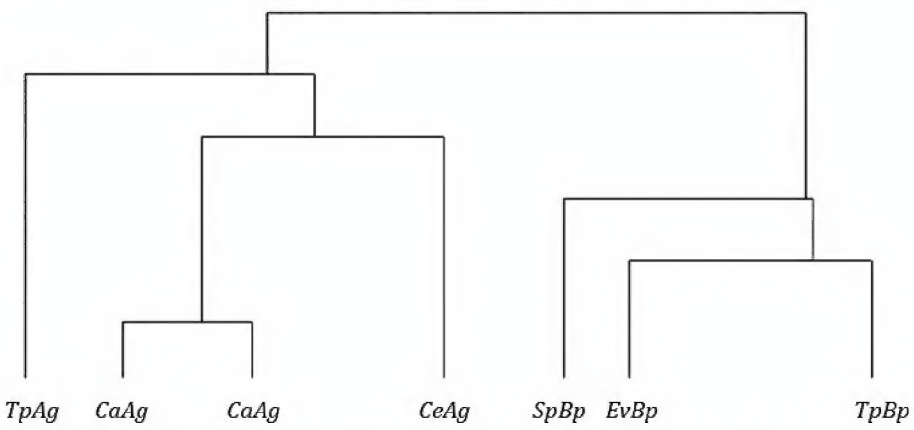


Figure 2. Dendrogram of the associations: TpAg (cluster 1) – *Thelypterido palustris-Alnetum glutinosae*; CaAg (clusters 2–3) – *Carici acutiformis-Alnetum glutinosae*; CeAg (cluster 4) – *Carici elongatae-Alnetum glutinosae*; SpBp (cluster 5) – *Salici pentandrae-Betuletum pubescentis*; EvBp (cluster 6) – *Eriophoro vaginati-Betuletum pubescentis*; TpBp (cluster 7) – *Thelypterido palustris-Betuletum pubescentis*.

The descriptions of the associations and classification scheme are presented below. We provide lists of the diagnostic species, synonyms, brief information on ecology, distribution, and community structure for each vegetation association. Only syntaxonomical names reported for Ukraine or described from its territory are listed as synonyms. The diagnostic species, supplemented with the phi coefficient (multiplied by 100), are listed in descending order of fidelity value. The synoptic table with the percentage frequency of the diagnostic species is presented in Table 1.

Annotated checklist of syntaxa

Descriptions of vegetation types

Cluster 1 – *Thelypterido palustris-Alnetum glutinosae* Klika 1940 mut. Kliment et al. 2022 (Figures 3, 4A; Table 1: column 1)

Table 1. Shortened synoptic table of the class *Alnetea glutinosae* in Ukraine: *Thelypterido palustris-Alnetum glutinosae* (TpAg), *Carici acutiformis-Alnetum glutinosae* (CaAg), *Carici elongatae-Alnetum glutinosae* (CeAg), *Salici pentandrae-Betuletum pubescentis* (SpBp), *Thelypterido palustris-Betuletum pubescentis* (TpBp) and *Eriophoro vaginati-Betuletum pubescentis* (EvBp); (b) indicates bryophytes; the numbers are percentage frequencies of the species; diagnostic species of individual associations are shaded and sorted by decreasing phi coefficient: dark grey shading indicates values of phi ≥ 0.5 and light grey shading 0.25 ≤ phi < 0.5; other species are sorted by decreasing frequencies; only species reaching a constancy of at least 25% in at least one vegetation type are shown; diagnostic species of higher syntaxa are marked with the following letters: A – *Alnion glutinosae*, B – *Betulion pubescentis*; SB – *Salici pentandrae-Betulion pubescentis*; see Suppl. material 4 for the full version of this table.

Phytosociological association		**TpAg**	**CaAg**	**CeAg**	**SpBp**	**TpBp**	**EvBp**
Number of plots		**113**	**273**	**142**	**71**	**185**	**149**
Thelypterido palustris-Alnetum glutinosae							
Sphagnum squarrosum (b)	A	43	1	5	16	9	2
Calliergon giganteum (b)	SB	35	3	7	19	6	.
Calliergonella cuspidata (b)	A	34	5	13	23	3	.
Sphagnum girgensohnii (b)	B	17	1	4	2	3	.
Carici acutiformis-Alnetum glutinosae							
Carex acutiformis	A	15	68	16	5	1	1
Carex riparia		12	47	15	.	2	3
Symphytum officinale		.	42	25	.	.	.
Calystegia sepium		1	33	16	.	.	.
Sium latifolium		3	28	8	.	.	.
Eupatorium cannabinum	A		22	10	2	.	.
Glechoma hederacea aggr.		1	12	1	.	.	.
Viburnum opulus		4	21	11	.	.	.
Sambucus nigra			12	3	.	.	.
Prunus padus subsp. *padus*	A	1	24	20	.	.	.
Lysimachia nummularia			15	8	.	.	.
Equisetum fluviatile	SB	4	27	15	3	9	1
Urtica dioica aggr.		4	64	25	3	.	.
Carici elongatae-Alnetum glutinosae							
Carex elongata	A	33	25	75	14	3	1
Thelypteris palustris	A	35	49	86	31	11	.
Filipendula ulmaria	A	11	37	60	5	.	.
Rubus idaeus		14	15	42	6	.	.
Caltha palustris	A	22	38	47	11	4	1
Dryopteris carthusiana	A	37	37	58	27	11	1
Plagiomnium affine aggr. (b)	A,SB	12	10	27	3	1	.
Geum rivale	A	12	9	24	.	.	.
Salici pentandrae-Betuletum pubescentis							
Molinia caerulea	SB	12	1	2	78	9	16
Agrostis canina		2	1	4	37	2	.
Thelypterido palustris-Betuletum pubescentis							
Carex lasiocarpa		27	1	1	45	97	56
Menyanthes trifoliata		44	10	21	34	78	13
Carex rostrata	B	9	1	2	16	31	5
Eriophorum gracile	B	3	.	.	5	39	3
Carex nigra	B	11	1	1	20	26	4
Rhynchospora alba		.	.	.	8	18	7
Eriophoro vaginati-Betuletum pubescentis							
Eriophorum vaginatum	B	2	.	.	3	24	95
Rhododendron tomentosum	B	.	.	.	3	28	67
Polytrichum strictum (b)	B	4	.	.	9	41	58
Sphagnum magellanicum (b)	B	4	.	.	6	27	46
Vaccinium uliginosum	B	.	.	.	3	11	25
Calluna vulgaris	B	.	.	.	2	2	15

Phytosociological association		TpAg	CaAg	CeAg	SpBp	TpBp	EvBp
Number of plots		**113**	**273**	**142**	**71**	**185**	**149**
Diagnostic species for more than one association							
Calamagrostis canescens	A	62	13	24	55	43	5
Humulus lupulus	A	3	50	40	.	.	.
Solanum dulcamara	A	19	61	59	6	1	.
Lycopus europaeus	A	34	64	65	22	12	.
Galium palustre	A	24	57	61	11	15	.
Iris pseudacorus	A	32	56	54	19	3	1
Ribes nigrum	A	4	29	30	.	.	.
Scutellaria galericulata	A	8	34	32	5	.	.
Stachys palustris		1	25	26	2	.	.
Vaccinium oxycoccos aggr.	B	3	.	.	17	82	81
Andromeda polifolia	B	1	.	.	8	54	58
Pinus sylvestris		25	1	2	56	81	87
Sphagnum recurvum aggr. (b)		15	1	.	28	99	93
Diagnostic species of high rank syntaxa							
Alnus glutinosa	A	100	100	100	23	2	1
Betula pubescens aggr.	SB,B	38	3	11	100	100	100
Frangula alnus	A,B	58	43	49	38	26	7
Vaccinium myrtillus	B	25	1	1	17	20	22
Carex appropinquata	SB	20	6	20	28	5	2
Lysimachia vulgaris	A	78	69	82	86	71	12
Sphagnum palustre aggr. (b)	B	43	2	11	45	31	11
Peucedanum palustre	A	34	19	25	38	38	3
Salix cinerea	A	58	49	46	41	44	15
Lysimachia thyrsiflora	A	30	23	24	34	41	4
Athyrium filix-femina	A	13	12	27	8	1	.
Other species							
Comarum palustre		40	12	29	53	59	4
Pleurozium schreberi (b)		18	4	15	23	43	34
Agrostis stolonifera aggr.		23	6	14	22	13	1
Phragmites australis		43	38	52	33	54	21
Calla palustris		34	11	31	14	19	5
Polytrichum commune (b)		30	3	11	23	42	23
Lythrum salicaria		23	34	32	9	6	.

Diagnostic species: *Sphagnum squarrosum* 41.4, *Calliergon giganteum* 32.6, *Calliergonella cuspidata* 27.4, *Sphagnum girgensohnii* 27.1, *Calamagrostis canescens* 26.7

Synonyms: *Sphagno squarrosi-Alnetum glutinosae* Solińska-Górnicka (1975) 1987 (art. 5); *Sphagno squarrosi-Alnetum* Solińska-Górnicka ex Prieditis 1997 (syntax. syn.); *Mnio affini-Alnetum glutinosae* Grygora, Vorobyov et Solomakha 2005 p.p (syntax. syn.)

Ecology: This association describes vegetation of oligotrophic alder carr forests on peaty nutrient-poor soils. It is related to low-lay areas, peaty river floodplains, edges of bogs, and mires. Highly waterlogged, low-productive substrates combined with local climatic conditions form the unique oligotrophic environment in which acidophilous species predominate and a high diversity of bryophytes develop. This vegetation was recorded in the forest zone of Ukraine, mainly in its northern part.

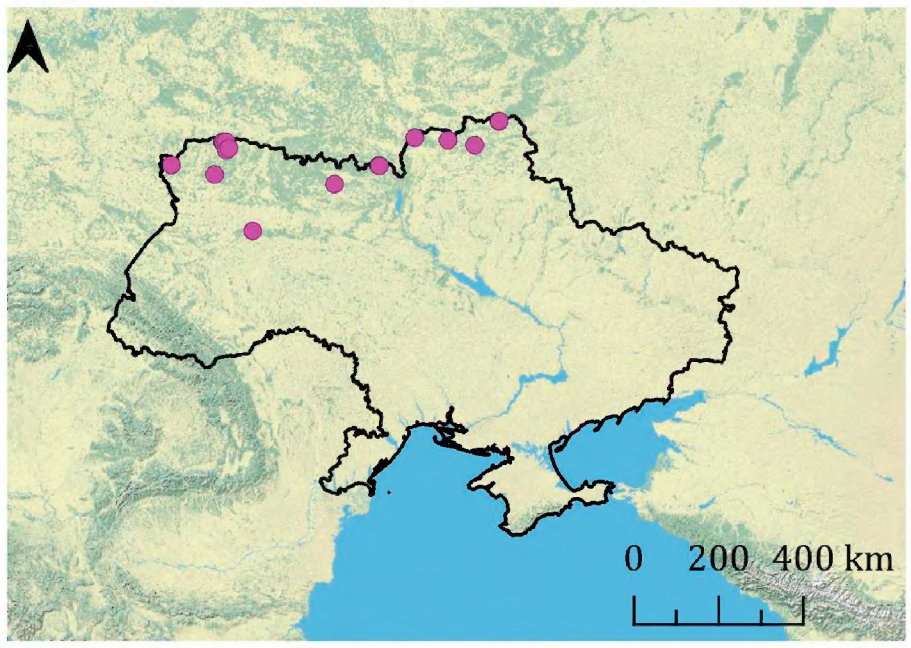
Structure and composition: The canopy is dominated by *Alnus glutinosa* mixed with *Betula pendula*, *B. pubescens* aggr., *Picea abies* and *Pinus sylvestris*. The shrub layer is species-poor and consists of *Frangula alnus*, *Salix aurita*, *S. cinerea*, *Sorbus aucuparia*, and *Viburnum opulus*. The herb layer is enriched with plants from different ecological groups: acidophilous species, sedges, ferns, and wetland plants with a broad tolerance to soil moisture and soil acidity fluctuations. A well-developed moss layer comprised of *Sphagnum* species accompanied by other bryophytes, the most frequent of which are *Aulacomnium palustre*, *Brachythecium rutabulum*, *Calliergon giganteum*, *Calliergonella cuspidata*, *Climacium dendroides*, *Dicranum polysetum*, *Hypnum cuppresiforme*, and *Plagiomnium affine* aggr.

Clusters 2–3 – *Carici acutiformis-Alnetum glutinosae* Scamoni 1935 (Figures 3, 4B; Table 1: column 2)

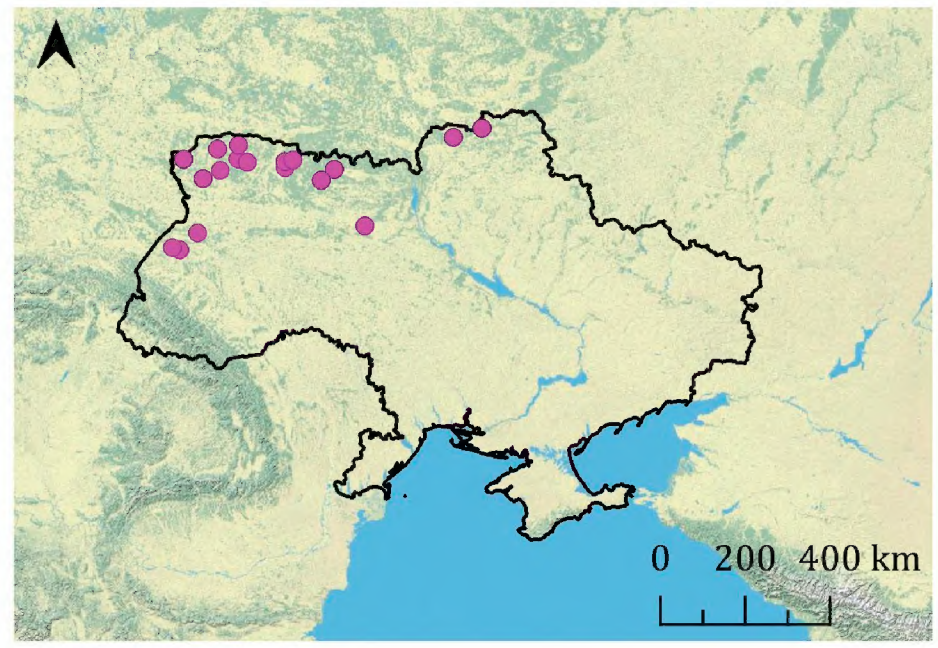
Diagnostic species: ***Carex acutiformis* 59.0**, *C. riparia* 45.4, *Symphytum officinale* 44.0, *Humulus lupulus* 42.9, *Urtica dioica* aggr. 41.3, *Calystegia sepium* 39.5,

Sium latifolium 39.3, *Solanum dulcamara* 38.2, *Eupatorium cannabinum* 32.0, *Lycopus europaeus* 29.4, *Galium palustre* 29.1, *Glechoma hederacea* aggr. 28.9, *Iris pseudacorus* 28.8, *Viburnum opulus* 28.7, *Sambucus nigra* 28.1, *Prunus padus* subsp. *padus* 27.6, *Scutellaria galericulata* 27.3, *Ribes nigrum* 27.3, *Lysimachia nummularia* 26.3, *Equisetum fluviatile* 25.9, *Stachys palustris* 25.1

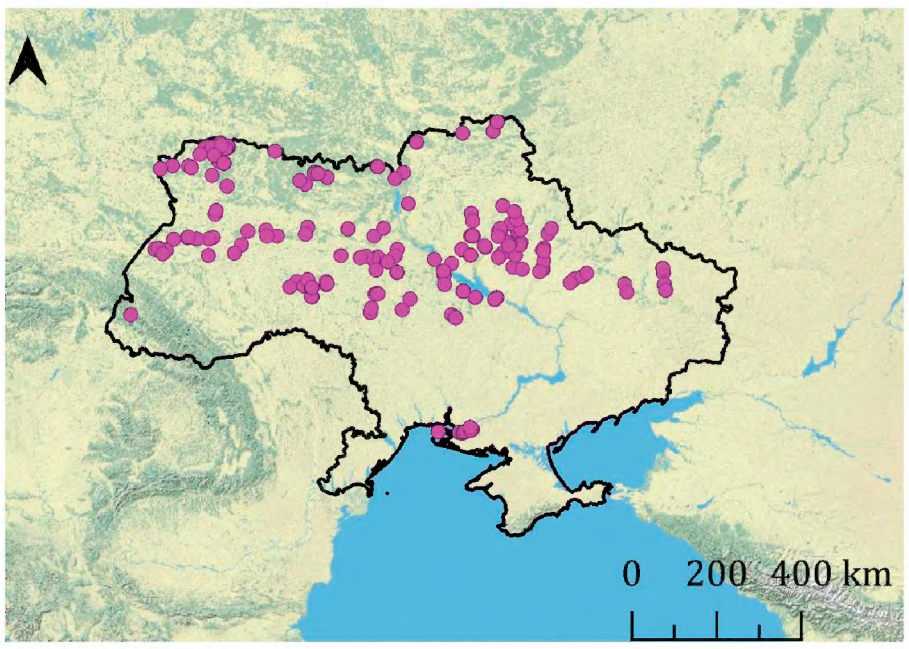
Synonyms: *Carici ripariae-Alnetum glutinosae* Weisser 1970 (syntax. syn); *Carici elatae-Alnetum glutinosae* Franz 1990 (art. 5); *Angelico sylvestri-Alnetum* Borhidi 1996 (syntax. syn.); *Cariceto pseudocyperi-Alnetum* Nazarenko, Kuzemko 2011 (art. 5, syntax. syn.); *Sio latifolii-Alnetum glutinosae* Vorobyov et I. Solomakha in I. Solomakha et al 2015 (syntax. syn.)



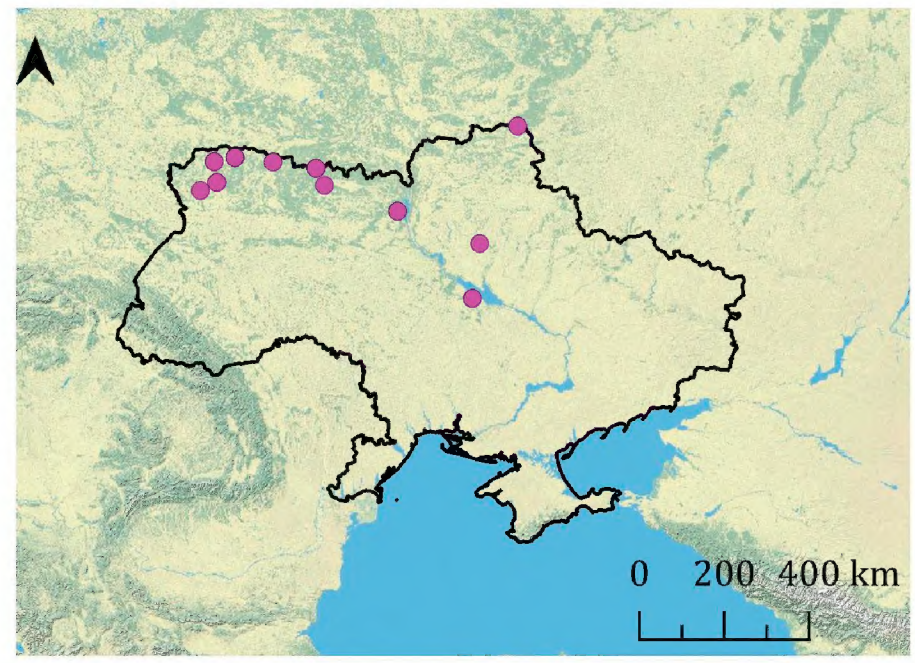
Thelypterido palustris-Alnetum glutinosae



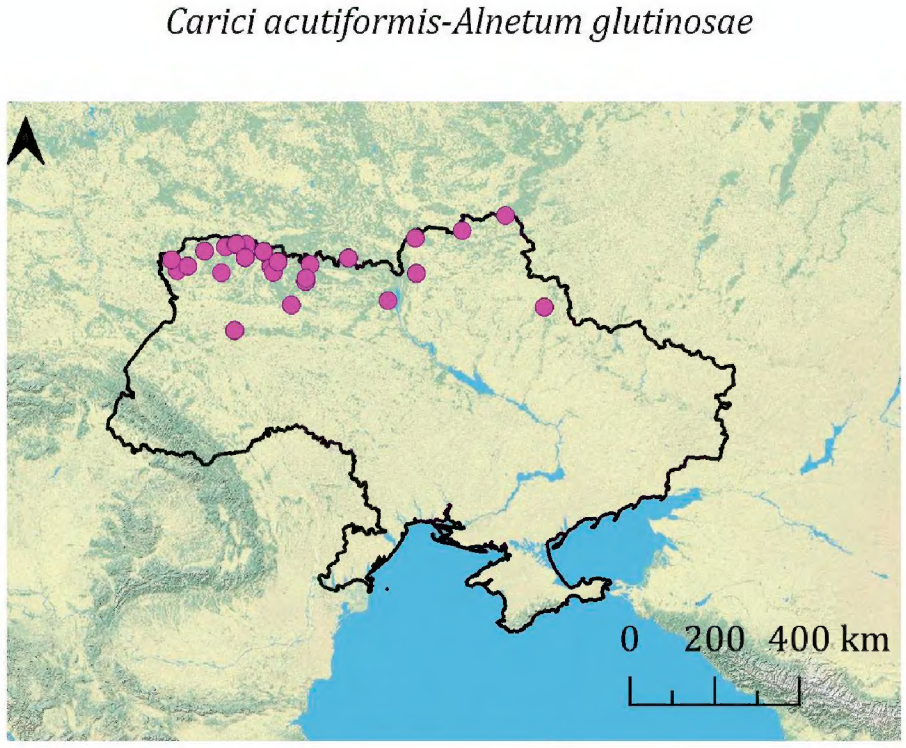
Carici elongatae-Alnetum glutinosae



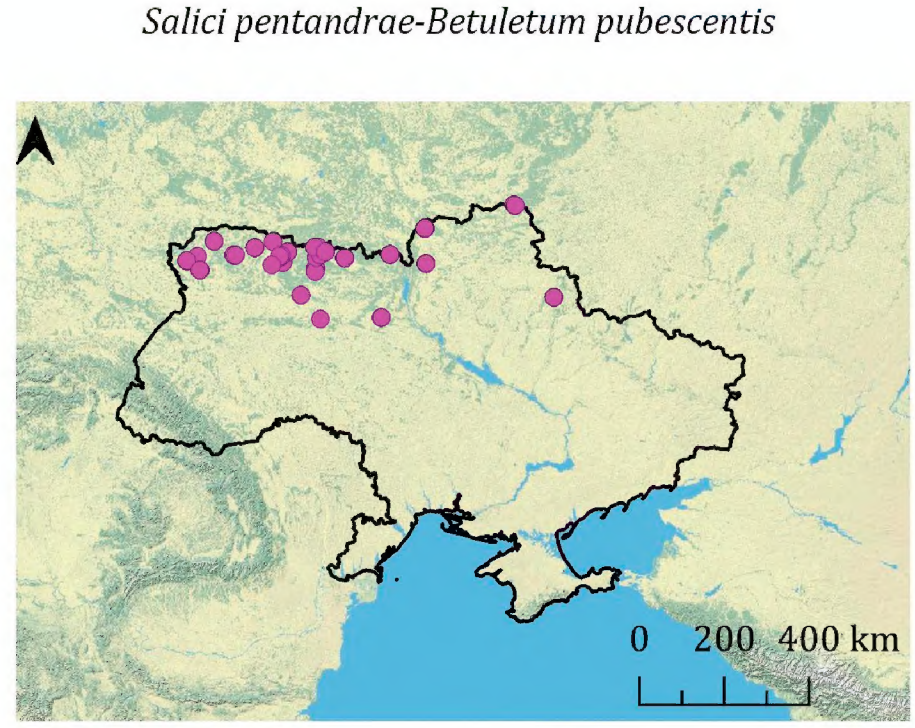
Carici acutiformis-Alnetum glutinosae



Salici pentandrae-Betuletum pubescentis



Thelypterido palustris-Betuletum pubescentis



Eriophoro vaginati-Betuletum pubescentis

Figure 3. Distribution of the associations of the class *Alnetea glutinosae* in Ukraine.

Ecology: The association includes eutrophic alder carr on moist muddy and clay swamps, sometimes peaty soils with periodical groundwater flooding. This vegetation is commonly found in water-logged floodplains, lowlands, along rivers, and in depressions on river terraces. The territorial distribution of this association is related to all physical-geographic zones of Ukraine.

Structure and composition: The canopy is dominated by *Alnus glutinosa* with an admixture of *Fraxinus excelsior*, *Populus alba*, *Salix alba*, and *Ulmus laevis*. The well-developed shrub layer is characterized by the frequent presence of *Coryllus avellana*, *Frangula alnus*, *Prunus padus* subsp. *padus*, *P. spinosa*, *Ribes nigrum*, *Sorbus aucuparia* and *Viburnum opulus*. The species-rich herb layer is composed of dominant tall sedges (*Carex acutiformis*, *C. riparia*, *Scirpus sylvaticus*) and an abundance of helophytes, hygrophytes, species of wet grasslands, and ferns. In some stands, the presence of climbing plants (*Aristolochia clematitis*, *Convolvulus arvensis*, *Fallopia dumetorum*, *Solanum dulcamara*) is conspicuous. The group of hygro- and mesophylous ruderal species (e.g. *Alliaria petiolata*, *Arctium lappa*, *Bidens tripartita*, *Echinocystis lobata*, *Impatiens parviflora*) is also a consistent component of this community. The few bryophytes (*Drepanocladus aduncus*, *Plagiomnium affine* aggr., *Pleurozium schreberi*, *Polytrichum commune*) inhabit the most humid shaded areas.

Cluster 4 – *Carici elongatae-Alnetum glutinosae* Schwickerath 1933 (Figures 3, 4C; Table 1: column 3)

Diagnostic species: ***Carex elongata* 52.7**, *Thelypteris palustris* 47.4, *Filipendula ulmaria* 47.4, *Rubus idaeus* 38.6, *Solanum dulcamara* 36.1, *Galium palustre* 33.2, *Lycopus europaeus* 31.1, *Humulus lupulus* 30.5, *Caltha palustris* 29.6, *Dryopteris carthusiana* 29.1, *Plagiomnium affine* aggr. 29.0, *Ribes nigrum* 27.7, *Geum rivale* 27.6, *Stachys palustris* 26.9, *Iris pseudacorus* 26.9, *Scutellaria galericulata* 25.5

Synonyms: *Calamagrostio canescenti-Alnetum glutinosae* Mikyška 1956 (syntax.syn.); *Ribo nigri-Alnetum* Solińska-Górnicka (1975) 1987 (art. 5, syntax. syn.)

Ecology: This association groups meso- to eumesotrophic alder carr on peat-clay soils with a high content of undecomposed organic matter. It develops on the water-logged depressions within central parts of the river floodplains or on the watershed plains. This community is reported from the forest zone and less frequently – in the northern part of the forest-steppe zone.

Structure and composition: The tree layer is always dominated by *Alnus glutinosa*. The well-developed shrub layer is composed of several species, the most frequent of which are *Frangula alnus* and *Salix cinerea*. The terrain of this vegetation is comprised of hummocks up to a height of 1 m and water-logged hollows 0.2–0.3 m deep. Such a mosaic of raised and low-lying areas is reflected in the structure of the herb layer. The drier hummocks host numerous ferns, sedges, hygrophytes and some mesophylous species. Water-logged hollows are usually inhabited by hydrophytes (*Hydrocharis morsus-ranae*, *Lemna minor*, *Spirodela polyrhiza*, *Utricularia vulgaris*) or amphibious plants (*Alisma plantago-aquatica*, *Hottonia palustris*, *Hydrocotile vulgare*, *Oenanthe aquatica*, *Rorippa amphibia*). The moss is comprised of diverse bryophytes (e.g *Brachythecium rivulare*, *B. rutabullum*, *Calliergon cordifolium*, *Calliergonella cuspidata*, *Climacium dendroides*, *Drepanocladus aduncus*, *Hypnum cuppresiforme*, *Polytrichum commune*). In contrast, *Sphagnum* mosses play a minimal role in the formation of the moss layer, particularly when compared to the association *Thelypterido palustris-Alnetum glutinosae*.

Cluster 5 – *Salici pentandrae-Betuletum pubescentis* Soó 1955 (Figures 3, 4D; Table 1: column 4)

Diagnostic species: *Molinia caerulea* 33.6, *Calamagrostis canescens* 32.3, *Agrostis canina* 28.8; *Sphagnum recurvum* aggr. 26.8

Synonyms: *Menyantho trifoliatae-Betuletum pubescentis* Grygora et al. 2005 p.p.; *Carici appropinquatae-Betuletum pubescentis* Grygora et al. 2005

Ecology: This association groups birch swamp forests on basiphylous soils enriched with carbonate compounds. The community has been documented across the forest zone of Ukraine.

Structure and composition: The canopy usually consists of *Betula pubescens* aggr. with a frequent admixture of *Alnus glutinosa*, *Betula pendula*, *Pinus sylvestris*, and *Populus tremula*. The dominant species of the shrub layer are *Frangula alnus*, *Salix cinerea*, *S. pentandra*, *Sorbus aucuparia*. The herb layer usually consists of *Carex* sp. div., species of mesotrophic mires and wet grasslands, often combined with ferns and hygrophilous plants. The moss layer tends to be well-developed and with numerous bryophytes plays a significant role in the community structure. Within the dominants are *Calliergon giganteum*, *Calliergonella cuspitata*, *Sphagnum palustre* aggr., *S. squarrosum* aggr.

Clusters 6 –*Thelypterido palustris-Betuletum pubescentis* Czerwiński 1972 (Figures 3, 4E; Table 1: column 5)

Diagnostic species: *Carex lasiocarpa* 54.7, *Sphagnum recurvum* aggr. 54.7, *Vaccinium oxycoccos* aggr. 51.5, *Menyanthes trifoliata* 42.1, *Andromeda polifolia* 37.7, *Pinus sylvestris* 35.6, *Carex rostrata* 29.6, *Eriophorum gracile* 29.6, *Carex nigra* 26.8, *Rhynchospora alba* 25.3

Synonyms: *Agrostio stoloniferae-Betuletum pubescentis* Grygora et al. 2005 p.p.; *Carici appropinquatae-Betuletum pubescentis* Grygora et al. 2005 p.p.; *Carici limosae-Betuletum pubescentis* Grygora et al. 2005 p.p.; *Menyantho trifoliatae-Betuletum pubescentis* Grygora et al. 2005 p.p.

Ecology: This association represents birch forests on water-logged peaty acidophilous soils. The vegetation is distributed mainly across the forest zone of Ukraine. Few localities have been documented in the north of the forest-steppe zone.

Structure and composition: The tree layer is dominated by *Betula pubescens* aggr. and *Pinus sylvestris*. The shrub layer consists mainly of *Salix cinerea* with a frequent admixture of *Frangula alnus*, *Salix aurita*, *S. repens*. In the herb layer an abundance of different hygrophilous species,

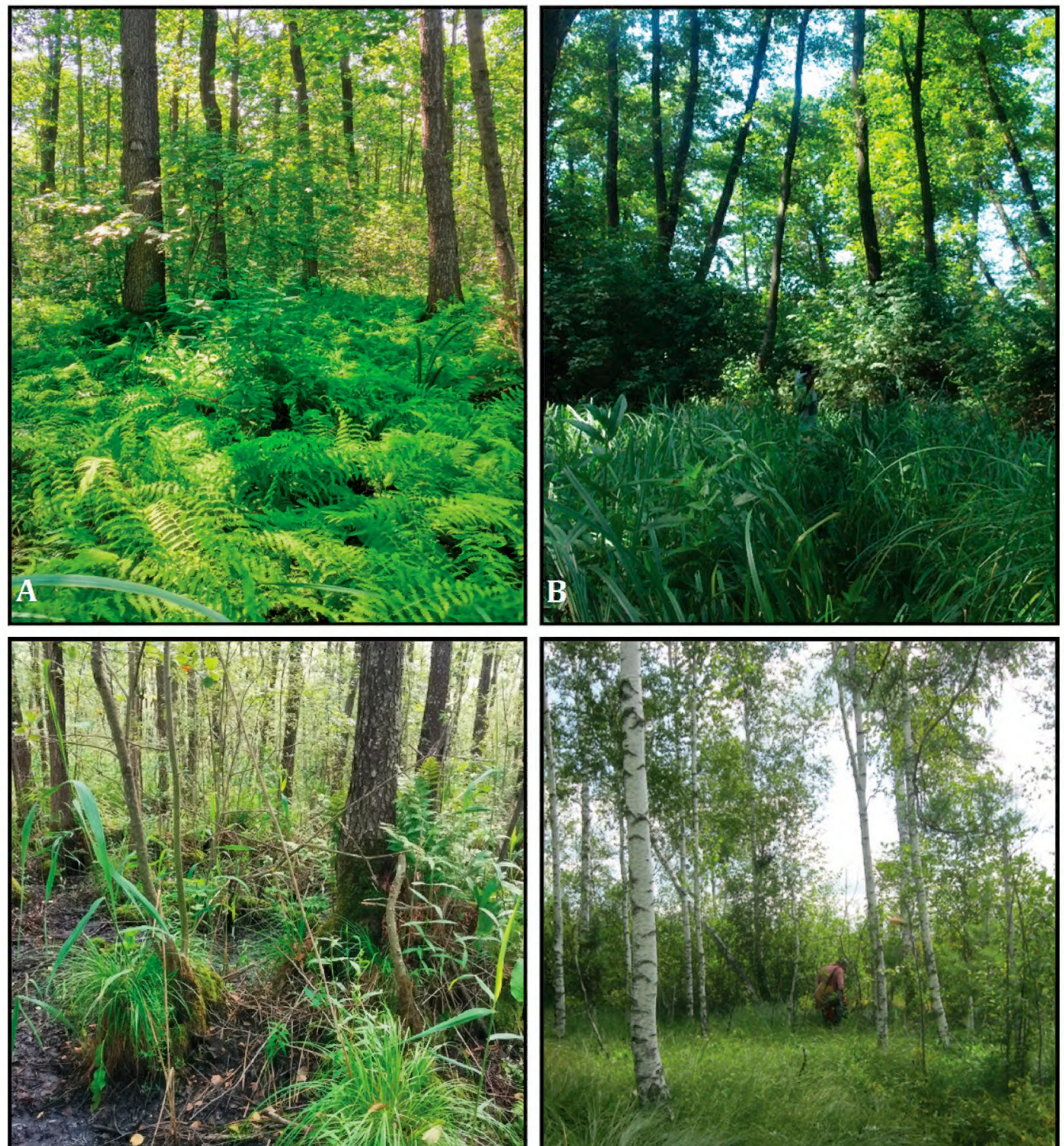


Figure 4. *Alnetea glutinosae* in Ukraine: (**A**) *Thelypterido palustris-Alnetum glutinosae*. Location: Volyn region, Lubeshiv district near Velyka Glusha village, Pryp'yat' River (8.07.2021); (**B**) *Carici acutiformis-Alnetum glutinosae*. Location: Kherson region, Gola Prystan district, near Stara Zbur'yivka, Dnipro River (19.07.2019); (**C**) *Carici elongatae-Alnetum glutinosae*. Location: Volyn region, Lubeshiv district near Grechyshcha village, Pryp'yat' River (7.07.2021); (**D**) *Salici pentandrae-Betuletum pubescentis*. Location: Rivne region, Rivne Natural Reserve (15.08.2018); (**E**) *Thelypterido palustris-Betuletum pubescentis*. Location: Rivne region, Rivne Natural Reserve (15.08.2018); (**F**) *Eriophoro vaginati-Betuletum pubescentis*. Location: Rivne region, Rivne Natural Reserve (15.08.2018). All photos by L. Borsukevych.

often accompanied by acidophilous sedges (*Carex appropinquata*, *C. cespitosa*, *C. elongata*, *C. lasiocarpa*, *C. limosa*, *C. nigra*), ferns and typical floristic elements of minerotrophic fens and raised bogs. A markedly developed moss layer is comprised of diverse *Sphagnum* species (*S. magellanicum*, *S. palustre* aggr., *S. recurvum* aggr.) together with *Calliergon giganteum*, *Dicranum rugosum*, *Pleurozium schreberi*, *Polytrichum commune*, *P. strictum*.

Cluster 7 – *Eriophoro vaginati-Betuletum pubescentis* (Hueck 1929) Passarge et Hofmann 1968 (Figures 3, 4F; Table 1: column 6)

Diagnostic species: *Eriophorum vaginatum 81.8*, *Rhododendron tomentosum 61.3*, *Vaccinium oxycoccos* aggr. *50.6*, *Sphagnum recurvum* aggr. 49.0, *Polytrichum strictum* 45.3, *Andromeda polifolia* 42.6, *Sphagnum magellanicum* 41.4, *Pinus sylvestris* 40.5, *Vaccinium uliginosum* 33.4, *Calluna vulgaris* 31.8

Synonyms: *Agrostio stoloniferae-Betuletum pubescentis* Grygora et al. 2005 p.p.; *Carici limosae-Betuletum pubescentis* Grygora et al. 2005 p.p.; *Menyantho trifoliatae-Betuletum pubescentis* Grygora et al. 2005 p.p.

Ecology: This association represents minerotrophic birch forests on the margins of peat bogs, shallow lakes, and depressions. The vegetation occupies the most waterlogged habitat with a stable water regime and deep peat soils. Its distribution is restricted to the forest zone of Ukraine, mainly to the northern part.

Structure and composition: These two-layered stands are always dominated by *Betula pubescens* aggr. with a significant proportion of *Pinus sylvestris* in the tree layer. The shrub layer usually is not developed. Sometimes it contains *Frangula alnus*, and juveniles of *Quercus robur*, *Picea abies*, and *Populus tremula*. The herb layer is dominated mainly by acidophilous species, such as *Carex lasiocarpa*, *Eriophorum vaginatum*, *Rhododendron tomentosum*, and *Vaccinium oxycoccos* aggr. There is a high percentage of moss cover in this vegetation which most frequently consists of *Aulacomnium palustre*, *Pleurozium schreberi*, *Polytrichum strictum*, *Sphagnum magellanicum*, *S. palustre* aggr. and *S. recurvum* aggr.

Syntaxonomic synopsis

Alnetea glutinosae Br.-Bl. et Tx. ex Westhoff et al. 1946
Alnetalia glutinosae Tx. 1937
Alnion glutinosae Malcuit 1929
1. *Thelypterido palustris-Alnetum glutinosae* Klika 1940 mut. Kliment et al. 2022
2. *Carici elongatae-Alnetum glutinosae* Schwickerath 1933
3. *Carici acutiformis-Alnetum glutinosae* Scamoni 1935

Salici pentandrae-Betuletalia pubescentis Clausnitzer in Dengler et al. 2004
Salici pentandrae-Betulion pubescentis Clausnitzer in Dengler et al. 2004
4. *Salici pentandrae-Betuletum pubescentis* Soó 1955

Sphagno-Betuletalia pubescentis Scamoni et Passarge 1959
Betulion pubescentis Lohmeyer et Tx. ex Oberd. 1957
5. *Thelypterido palustris-Betuletum pubescentis* Czerwiński 1972
6. *Eriophoro vaginati-Betuletum pubescentis* (Hueck 1929) Passarge et Hofmann 1968

Ordination

The NMDS ordination (Figure 5) supported the ecological interpretation of the defined vegetation units by distinguishing two main groups of plots. Birch forests were separated from alder carr along the first NMDS axis, demonstrating significant differences in the floristic composition of the communities, firstly due to the proportion of acidophilous species. The variations in the nutrients, soil acidity, and the associated moisture regime determine the ecological differentiation of the communities within the class *Alnetea glutinosae*. The ordination diagram clearly shows the spread of the defined vegetation associations along the first axis, from the most mesophilous *Carici acutiformis-Alnetum glutinosae* to the most acidophilous *Eriophoro vaginati-Betuletum pubescentis*, which develops under stagnant moisture conditions. There is no sharp separation between the associations of the alliance *Alnion glutinosae*. This is due to the frequent presence of many hygrophilous species of broad ecological amplitude across all communities of the alliance. However, each of the defined vegetation types has its floristic characteristics reflected in the set of diagnostic species.

The difference between vegetation types of the class *Alnetea glutinosae* was also reflected in the mean EIVs (Figure 6). The most significant effects on the species composition of vegetation associations are soil moisture, soil reaction, nutrients, and light regime. The most evident difference was in the distribution of indicator values for soil acidity and nutrients. Thus, the birch forests occur in more acidic sites with a low nutrient content. Such a specific soil environment, combined with stagnant moisture, is unfavorable for the development of a closed productive canopy, and contribute to these birch forests being more open, well-lit habitats than alder carr. Simultaneously, the vegetation of *Alnetea glutinosae* does not differ significantly at the level of associations in terms of soil moisture, but it differs significantly at the level of alliances.

Discussion

Syntaxonomy

We analysed the vegetation plots from a large phytosociological database to allow us to undertake a critical overview of the syntaxonomy of the class *Alnetea glutinosae* in Ukraine. The proposed scheme is consistent with recent regional studies in dividing the class into alliances (Hrivnák et al. 2021; Koljanin et al. 2023). It is worth noting that, in general, a semblance of consensus has already been reached in the discussions on the structure of the *Alnetea glutinosae*

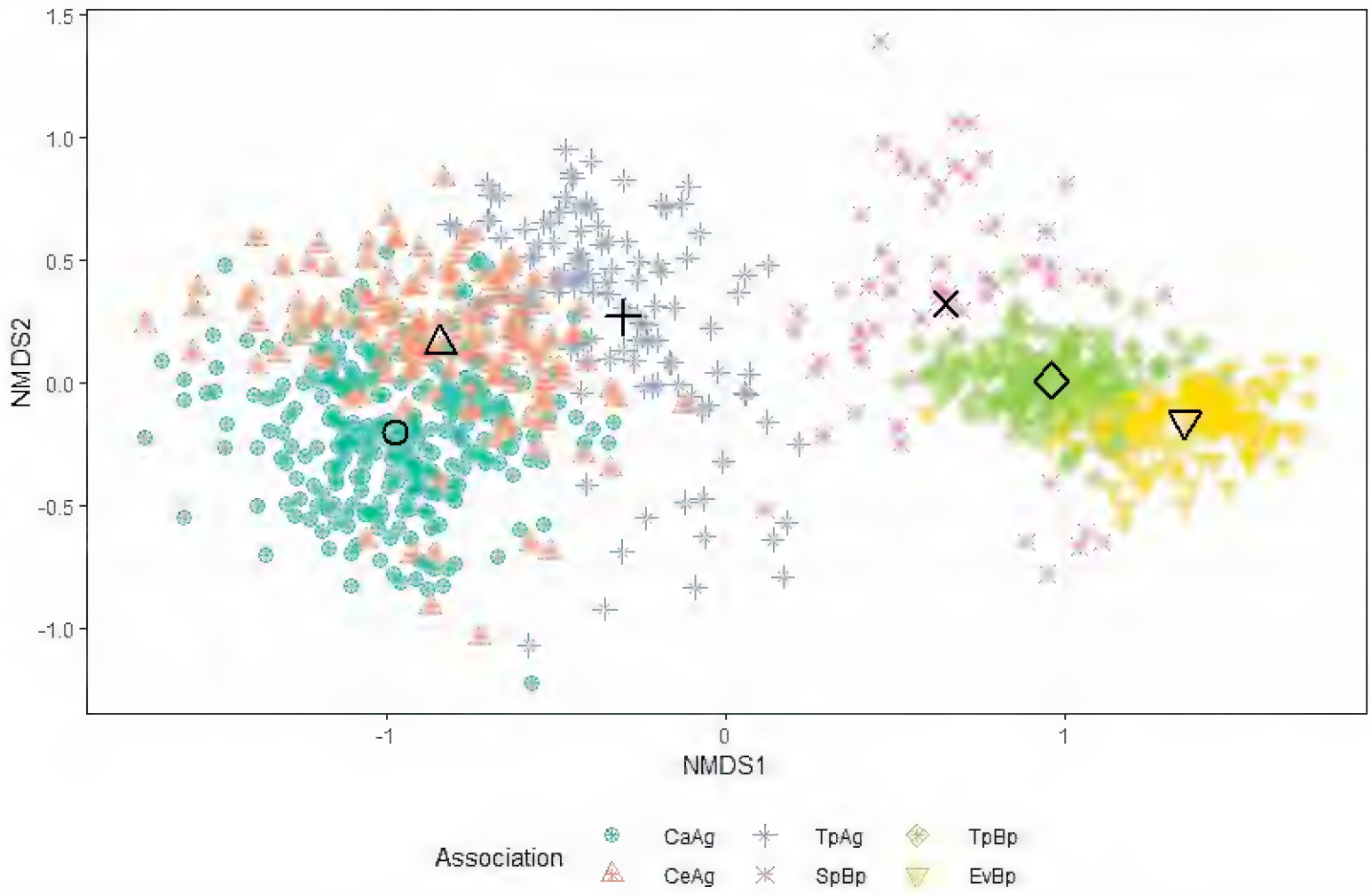


Figure 5. NMDS ordination of the plots assigned to the class *Alnetea glutinosae*. Colored shapes indicate different associations: *Carici acutiformis-Alnetum glutinosae* (CaAg), *Carici elongatae-Alnetum glutinosae* (CeAg), *Thelypterido palustris-Alnetum glutinosae* (TpAg), *Salici pentandrae-Betuletum pubescentis* (SpBp), *Thelypterido palustris-Betuletum pubescentis* (TpBp) and *Eriophoro vaginati-Betuletum pubescentis* (EvBp). Enlarged black shapes correspond to the centroids of each association.

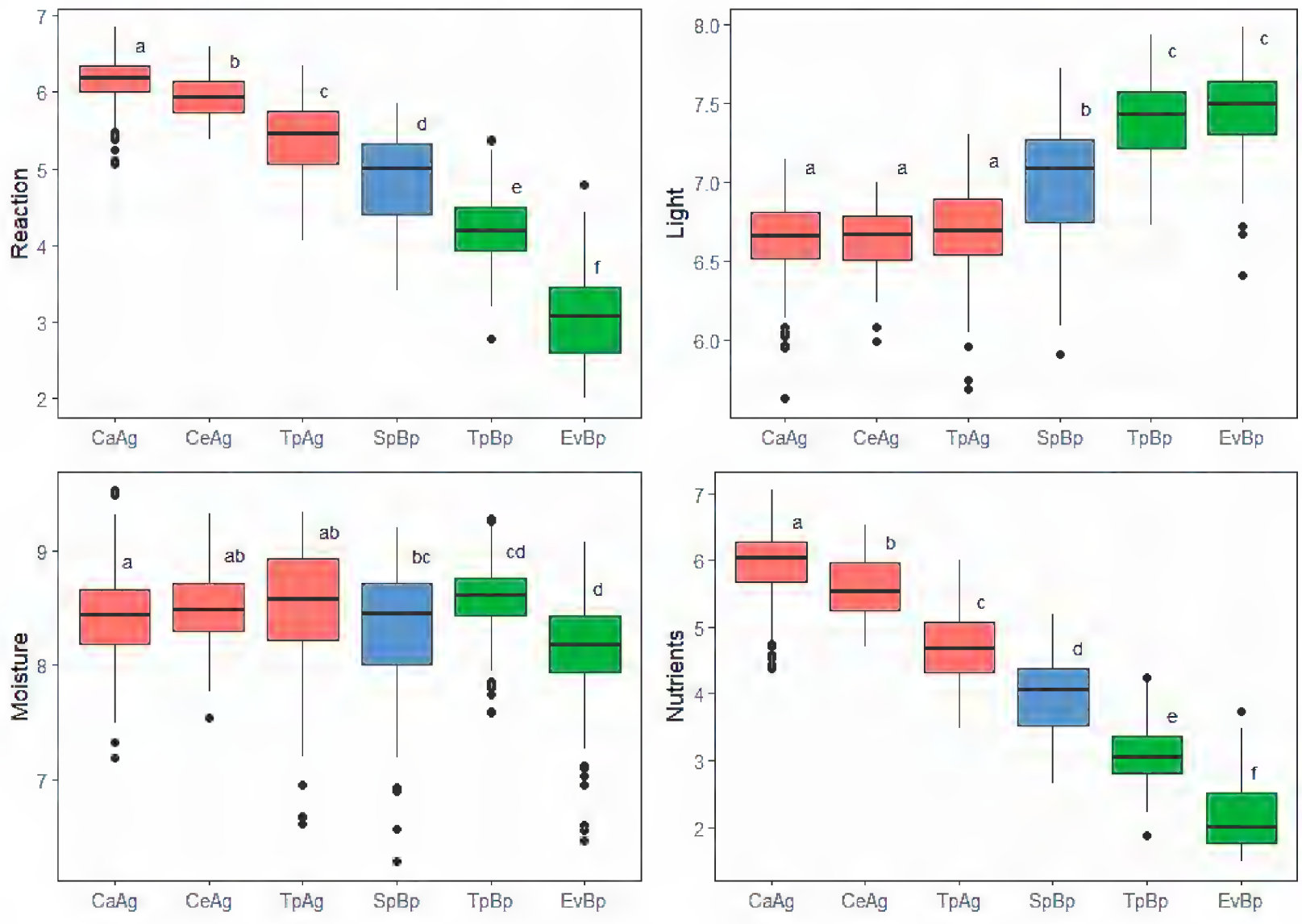


Figure 6. Boxplots of EIVs for each association: *Carici acutiformis-Alnetum glutinosae* (CaAg), *Carici elongatae-Alnetum glutinosae* (CeAg), *Thelypterido palustris-Alnetum glutinosae* (TpAg), *Salici pentandrae-Betuletum pubescentis* (SpBp), *Thelypterido palustris-Betuletum pubescentis* (TpBp) and *Eriophoro vaginati-Betuletum pubescentis* (EvBp). Boxes indicate the interquartile range, bold lines represent the median, and whiskers indicate the range of values, black dots indicate outliers. Different letters express the significance of the differences between group means at $p < 0.05$ according to Tukey's test. Colors refer to alliances: red – *Alnion glutinosae*; blue – *Salici pentandrae-Betulion pubescentis*; green – *Betulion pubescentis*.

and its syntaxonomic interrelation with ecologically similar types of vegetation. Especially after the publication of the EVC (Mucina et al. 2016), where new syntaxonomic suggestions were agreed upon to distinguish between the riparian gallery forests, floodplain willow scrub, alder and willow carrs. These vegetation types are now considered within four phytosociological classes, respectively – *Alno glutinosae-Populetea albae*, *Salicetea purpurea*, *Alnetea glutinosae* and *Franguletea*. Nevertheless, various researchers still share different opinions on the *Alnetea glutinosae* structure at the association level. In this context, we fully agree with the suggestion of Willner (2024) that a coherent classification and a harmonization of positions in scientific discussions on the classification of forest vegetation, including *Alnetea glutinosae*, should be based primarily on the principle of using trees and shrub species to define the orders and alliances and variability of herb and cryptogam layer to define the lower vegetation units.

The results of our research are somewhat different from those suggested for Europe (Douda et al. 2016). Excluding the vegetation of the *Leucojo aestivi-Fraxinetum angustifoliae* Glavač 1959 and *Carici lusitanicae-Alnetum glutinosae* Díaz et Pietro 1994, which are common in the Mediterranean region and do not occur in Ukraine, our research generally confirmed the separation of alder carr into three distinct types based on the nutrient levels. According to Douda et al. (2016), they are represented by different associations. The *Sphagno palustris-Alnetum glutinosae* Lemée 1937 unites oligotrophic peatland vegetation dominated by *Alnus glutinosa*, *Carici elongatae-Alnetum glutinosae* Tüxen 1931 represents mesotrophic alder swamp forests and *Carici ripariae-Alnetum glutinosae* Weisser 1970 combines eutrophic alder carr. A thorough review of the publications in which the syntaxa were initially documented, including nomenclatural verification and comparison with our data and regional surveys, resulted in some disagreements and suggestions that we will elaborate on below.

We propose that the name *Sphagno palustris-Alnetum glutinosae* adopted by Douda and co-authors (2016) for oligotrophic alder carr of the nemoral zone of Europe is not quite accurate. Instead, we agree with Hrivnák et al. (2021) who suggest that such communities should be considered under the association *Thelypterido palustris-Alnetum glutinosae*. Lemée (1937) proposed the name *Sphagno palustris-Alnetum glutinosae* for stands dominated by *Salix cinerea* and *Betula pubescens* found in central France. Within these stands *Alnus glutinosa* was listed for only two vegetation plots with low percentage cover. The floristic composition of the herb layer was dominated by Atlantic species *Blechnum spicant*, *Carex laevigata*, *Lonicera periclymenum*, *Osmunda regalis*, and *Scutellaria minor*. Only a few frequent components of alder carr such as *Galium palustre*, *Hydrocotyle vulgaris*, *Juncus effusus*, and *Molinia caerulea*, accompanied by some ferns (*Athyrium filix-femina*, *Dryopteris carthusiana*, *D. dilatata*), were noted. Lemée sampled this vegetation along the banks of streams on calcareous soils. The author pointed out that the community was ecologically close to the vegetation enriched with species of forest springs which he described in the same publication under the name of "*Alneto-Caricetum remotae*". Meanwhile, swamp forests with a developed layer of black alder, a multicomponent herb layer with a significant number of acidophilous species and sphagnum mosses were described by Klika (1939–1940) as the association *Thelypterido palustris-Alnetum glutinosae*. Solińska-Górnicka (1987) described this vegetation as the association *Sphagno squarrosi-Alnetum glutinosae*. Since the name *Thelypterido palustris-Alnetum glutinosae* has priority over the later names proposed by other authors, we recommend that it is used to indicate oligo- and meso-oligotrophic alder carr with a developed moss layer.

We consider that the name *Carici elongatae-Alnetum glutinosae*, with the author citation Tüxen 1931, is mistakenly assigned to mesotrophic alder carr. Tüxen (1931) used this name to indicate a community that differed significantly in species composition from mesophilous swamp forests. The alder forests he identified were predominantly composed of frequent mesophilous forest species (e.g. *Brachypodium sylvaticum*, *Carex sylvatica*, *Circaea lutetiana*, *Primula elatior*, *Stachys sylvatica*). Furthermore, the name of the association was published invalidly, as the author provided only species lists for the studied localities. For these reasons, Dengler et al. (2004) attempted to validate the name by choosing the neotype from the publication of Passarge (1960). However, the chosen phytosociological relevé, as a nomenclature type, did not reflect the floristic composition of the community described by Tüxen as *Carici elongatae-Alnetum glutinosae*. Instead it reflected the species composition of those communities that were published under this community name by many syntaxonomists to specify mesophilous swamp forests. The first author who described mesophilous alder carr under the name *Carici elongatae-Alnetum glutinosae* was Schwickerath (1933), and we accept this author of the association in our study.

We disagree with Douda et al. (2016) that the *Carici elongatae-Alnetum glutinosae* is a synonym for the *Carici acutiformis-Alnetum glutinosae*. In terms of ecological environment, species composition, and physiognomic differentiation, the vegetation of alder carr dominated by tall sedges (*Carex acutiformis*, *C. elata*, *C. riparia*) is quite different. It has a less pronounced microrelief and develops in conditions of lower soil humidity. The herb layer is made up of common eutrophic hygrophilous species and not of acidophilous plants. The floristic and ecological separation of these two communities was also supported by a thorough review of the phytosociological publications, including the protologues of both associations (Schwickerath 1933; Scamoni 1935). For this reason, we consider *Carici elongatae-Alnetum glutinosae* and *Carici acutiformis-Alnetum glutinosae* as independent associations. We also believe that the name *Carici ripariae-Alnetum glutinosae*, considered by Douda et al. (2016) to group the eutrophic black alder swamps, is a later synonym of the *Carici acutiformis-Alnetum glutinosae*.

Based on the outcomes of our study, we suggest significant modifications to the content and structure of the class

Alnetea glutinosae at the national level in Ukraine. First of all, we follow the authors of the EVC (Mucina et al. 2016) and suggest including birch swamp forests which had previously been classified within the separate phytosociological class *Molinio-Betuletea pubescentis* Passarge in Passarge et G. Hofmann 1968 (Passarge and Hofmann 1968; Dubyna et al. 2019) in the *Alnetea glutinosae*. We also made some adjustments at the association level. Dubyna et al. (2019) reported ten phytosociological associations within the alliance *Alnion glutinosae* for the territory of Ukraine. We believe that there are only three associations within the alliance *Alnion glutinosae* present in Ukraine. Our conclusions are derived from the classification of a representative dataset, which has allowed us to distinguish well-defined vegetation types in terms of species composition and ecological conditions. In our study we assumed a broad concept of association range, therefore a slight difference in species composition was not a reason to designate a new association. We have also aggregated some associations that differ in the dominant species of the herb layer, for instance, tall sedges. Thus, we consider most of the associations listed in the "Prodrome of the Vegetation of Ukraine" (Dubyna et al. 2019) to be synonyms with *Thelypterido palustris-Alnetum glutinosae*, *Carici elongatae-Alnetum glutinosae*, or *Carici acutiformis-Alnetum glutinosae*.

It is our opinion that two associations suggested by Dubyna et al. (2019) as belonging to the class *Alnetea glutinosae*, should be referred to as the alliance *Alnion incanae*. These are *Urtico dioicae-Alnetum glutinosae* Scamoni 1935 and *Syringo josikaeae-Alnetum glutinosae* Felbaba-Klushyna 2010. The association *Urtico dioicae-Alnetum glutinosae* was not reported in the pan-European survey either within the vegetation of alder carr or the vegetation of the floodplain forests (Douda et al. 2016). However, it was mentioned as a part of the *Alnetea glutinosae* in a few regional (Oberdorfer 1992; Geißelbrecht-Taferner and Wallnöfer 1993) and local (Fukarek 1961; Dubyna and Dziuba 2014; Wartena and Ewald 2020) studies. Our study showed that the *Urtico dioicae-Alnetum glutinosae* is distinguished from alder carr by a substantial proportion of mesophilous species and acidophilous species of deciduous forests. It is therefore floristically and ecologically more similar to the vegetation of floodplain forests. Regarding the association *Syringo josikaeae-Alnetum glutinosae*, which is described only for the territory of Transcarpathia, more detailed research is required to get a better understanding of its species composition, structure, and syntaxonomic position. According to our results, the plots of this vegetation type were dispersed among the clusters that we have identified to be *Alnion incanae*. Therefore, at this point, we propose to exclude *Syringo josikaeae-Alnetum glutinosae* from the class *Alnetea glutinosae*. In addition, if the status of a separate phytosociological association can be verified, the name should be published according to ICPN rules. The current name *Syringo josikaeae-Alnetum glutinosae* Felbaba-Klushyna 2010 is invalid according to articles 2b and 5.

When discussing the syntaxonomy of the birch forests, it is important to note that this vegetation is the subject of targeted phytosociological research in Europe, which should produce a consistent classification at the level of associations, as has already been done for the floodplain forests (Douda et al. 2016) and other vegetation types (Landucci et al. 2020; Kalníková et al. 2021; Peterka et al. 2023). Furthermore, these studies are needed to validate the syntaxonomic structuring of the *Alnetea glutinosae* proposed in the EVC (Mucina et al. 2016) concerning the classification of birch swamp forests within the aforementioned class. In Ukraine, there are very few studies on birch swamp forests and they have been carried out within the forest zone. The researchers' efforts have led to the identification of five vegetation associations: *Agrostio stoloniferae-Betuletum pubescentis* Grygora et al. 2005, *Carici appropinquatae-Betuletum pubescentis* Grygora et al. 2005, *Carici limosae-Betuletum pubescentis* Grygora et al. 2005, *Menyantho trifoliatae-Betuletum pubescentis* Grygora et al. 2005, and *Sphagno magellanici-Betuletum pubescentis* Grygora et al. 2005 (Grygora et al. 2005). The authors, who reviewed this vegetation for the "Prodrome of the Vegetation of Ukraine" (Dubyna et al. 2019), decided to assign all the birch forests of Ukraine to the single association *Menyantho trifoliatae-Betuletum pubescentis* Grygora et al. 2005, which was classified within the alliance *Betulion pubescentis*, representing acidophilous birch swamp forests. Based on the results of our analysis, we conclude that there are two acidophilous communities of birch swamp forests in Ukraine – *Thelypterido palustris-Betuletum pubescentis* and *Eriophoro vaginati-Betuletum pubescentis*.

Our study has confirmed the presence of the alliance *Salici pentandrae-Betulion pubescentis* in Ukraine. This alliance was first documented in Ukraine by Vorobyov et al. (2016) who studied vegetation with *Betula pubescens* in the central section of the Dnipro Valley. However, the vegetation plots given by the authors in the publication and included in our analysis were assigned to clusters representing alder carr. Vorobyov et al. (2016) stated that the floristic composition of the vegetation they studied is very similar to black alder swamps and attributed this vegetation to the alliance *Salici pentandrae-Betulion pubescentis*, based only on the principle of physiognomical similarity and the absence of acidophilous species.

Distribution patterns of the class *Alnetea glutinosae* in Ukraine

Our study shows that the class *Alnetea glutinosae* within Ukraine is distributed across all physical-geographic zones. The main areas for this vegetation type are concentrated in the forest and the forest-steppe zones. In the south of Ukraine, swamp forests are localized in protected areas or floodplains of large rivers with a more or less preserved natural hydrological regime. The vegetation's distribution follows the distribution of the rivers in combination with local soil and climatic conditions.

To the west, the geographical distribution of the class *Alnetea glutinosae* reaches the swamp areas in the

floodplain of the Marusia river in the Lviv region. Toward the east, *Alnetea glutinosae* extends up to the Kharkiv region, where it has been reported from the floodplain of the Oskil river in the territory of Dvorichanskyi NNP. Within Ukraine the northernmost points of distribution for the *Alnetea glutinosae* are wetland areas located in NNP "Prypiat-Stokhid" (near Skorin' Lake, Volyn region), Rivne Nature Reserve, The Chornobyl Radiation and Ecological Biosphere Reserve (floodplain of Pryp'yat' River, Kyiv region), and NNP "Desna-Stara Huta" (floodplain of Vulytsia River, Sumy region). The boundaries for the *Alnetea glutinosae* distribution in the north, west, and east are rather artificial, as we followed the administrative boundaries within the study area. In Ukraine, alder and birch swamp forests are part of a continuum for this vegetation type in the nemoral zone of Eurasia. Of interest is the southern limit for the distribution of the class. Its distribution to the south is significantly limited by the absence of the appropriate soil and hydrological conditions. This is due not only to the increasing aridity of the climate, accentuated by global warming, but also due to significant changes in the hydrological regime of the rivers as a result of reclamation and the construction of hydroelectric plants during the 20th century (Didovets et al. 2020; Ovcharuk et al. 2020; Vyshnevskyi and Kutsiy 2022). Currently, the alder carr in the steppe zone can only be found within the floodplains of large rivers such as Southern Bug, Siversky Donets, and Dnipro. Within the Dnipro estuary region, we and other researchers (Dubyna and Dziuba 2014; Solomakha et al. 2015) have documented the southernmost localities for the *Alnetea glutinosae*. They are located on the territories of NNPs "Lower Dnipro" (Kherson region) and "Ivory Coast of Sviatoslav" (Mykolayiv region)

In terms of the distribution of individual vegetation types, only the occurrence of birch swamp forests is limited to the forest zone of Ukraine. The geographical range of the *Thelypterido palustris-Betuletum pubescentis* and *Eriophoro vaginatae-Betuletum pubescentis* are restricted to the northernmost regions of Ukraine. The distribution of the single association of the alliance *Salici pentadrae-Betulion pubescentis* (*Salici pentandrae-Betuletum pubescentis*), according to our dataset, is found across the forest zone. Preislerová et al. (2022) citing this alliance for the study area, indicated a relatively broad geographical range for this vegetation, covering the entire territory of Ukraine, except for Crimea. Our research does not support this statement. The distribution of birch swamp forests in the south is unlikely due to unfavorable conditions for their development within the steppe zone.

We documented the *Thelypterido-Alnetum glutinosae* and *Carici elongatae-Alnetum glutinosae* from scattered localities within the forest and northern forest-steppe zones. The vegetation of the *Carici acutiformis-Alnetum glutinosae* is the most frequent alder swamp forest in Ukraine.

We don't have any data on the distribution of the *Alnetea glutinosae* in Crimea. We were unable to organize our field research on the peninsula due to its occupation by Russia in 2014. There is also no relevant data in the literature. However, *Alnetea glutinosae* was reported in the vegetation of Crimea by Korzhenevskyi et al. (2003). The authors have mentioned two associations *Clemato vitalbae-Alnetum glutinosae* and *Ornithogalo pontici-Alnetum glutinosae* described by Didukh (1996). But this vegetation is more similar in its floristic composition to alder riparian floodplain forests. For this reason, in the last vegetation survey of Ukraine (Dubyna et al. 2019), these associations were classified as a part of the alliance *Alnion incanae*. Douda and co-authors (2016) also assigned this vegetation to this phytosociological alliance.

When assessing the distribution of vegetation plots across the study area we conclude that the *Alnetea glutinosae* class in Ukraine is well-documented and the results presented during our study are based on a geographically representative data set. However, further efforts are needed to digitize available data from different sources. Special attention should be paid to the historic records, mostly stored in personal archives, which will form the basis for further research on the dynamics of swamp forests, including the impacts of climate change, plant invasion, military actions, etc.

When discussing the current distribution of the *Alnetea glutinosae* in Ukraine, it should be noted that some of the phytosociological data analyzed during this study are historical and may no longer be relevant for their localities. We believe that birch swamp forests require more detailed research, in particular, to clarify their syntaxonomical variability and precise territorial distribution within Ukraine. However, in the context of the ongoing Russian aggression, such research is impossible as large areas within the forest zone are closed to all but military activity. In addition, such research is currently impossible for security reasons. Research on *Alnetea glutinosae*, as well as other vegetation, in Crimea, is also not possible at this moment in time.

Conclusions

The present work is the first synthetic study of the class *Alnetea glutinosae* in Ukraine based on a large phytosociological database. The geographical coverage of the dataset used in our study has allowed us to present a relatively complete review of the alder carr and birch wooded mires in Ukraine.

Using unsupervised classification we have distinguished six vegetation associations of the class *Alnetea glutinosae* within Ukraine. Our study has also allowed us to characterize the distribution of the vegetation associations, identify their diagnostic, constant and dominant species based on a consistent approach, and highlight the main environmental drivers determining vegetation differentiation and variability.

Our study has critically revised the previous syntaxonomic structure for the class *Alnetea glutinosae* in

Ukraine. The modifications we have proposed include the exclusion of two and the synonymization of seven vegetation associations. We have also introduced two vegetation associations of acidophilous birch forests to replace one, confirmed the presence of the basiphilous birch forests, and determined precisely the geographical range of this vegetation in Ukraine.

Our results could be a useful tool for biodiversity conservation, management planning, and habitat monitoring and mapping. We believe that this study is a step towards the development of formal definitions for the vegetation units proposed during this study and summarized in our classification. We hope that this study will be an important contribution to the production of a formalized classification system for the vegetation of Ukraine.

Data availability

A list of the data used for this publication is provided in Suppl. material 1. All analyzed relevés are available on request through the Ukrainian Wetland Database (Global Index of Vegetation-Plot Databases, ID: EU–UA–012) and the Database of the Floodplain Forests of Ukraine (by direct request to L. Borsukevych via lborsukiewicz@gmail.com).

Author contributions

SI and LB planned the research, LB and SI conducted the field sampling, SI performed the statistical analyses and led the writing, SI and LB prepared the tables, Appendix 1 and Suppl. materials 1–5. All authors critically revised the manuscript.

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Appendix 1

Syntaxonomic outline and nomenclature of the class *Alnetea glutinosae* in Ukraine.

The names, definitions and concepts of the higher syntaxonomic units (alliances, orders) follow Mucina et al. (2016). Diagnostic species were defined as those for which the phi coefficient (Chytrý et al. 2002) was ≥0.25, for highly diagnostic phi coefficient was exceeding 0.5. Species with frequency ≥ 25% were consider as constant, with frequency > 50% as highly constant. Dominant species were defined as those occurring with cover value > 25% in at least 10% of the plots. Highly diagnostic and highly constant species are given in bold. All diagnostic, constant and dominant species listed alphabetically.

***Alnetea glutinosae* Br.-Bl. et Tx. ex Westhoff et al. 1946**

European mesotrophic regularly flooded alder carr and birch wooded mires.

***Alnetalia glutinosae* Tx. 1937**

European mesotrophic regularly flooded alder carr

***Alnion glutinosae* Malcuit 1929**

European mesotrophic regularly flooded alder carr

Name giving taxon: *Alnus glutinosa* (Linnaeus) Gaertner 1790

Nomenclatural type: association à *Alnus glutinosa* Malcuit 1926 (*holotypus*) (Malcuit 1929)

Association ***Thelypterido palustris-Alnetum glutinosae* Klika 1940 mut. Kliment et al. 2022**

Name giving taxa: *Alnus glutinosa* (Linnaeus) Gaertner 1790, *Thelypteris palustris* Schott 1834

Original form of the name (Klika 1939–1940)**:** "*Alnus glutinosa-Dryopteris thelypteris*-Assoziation" (p. 99)

Nomenclatural type: (Klika 1939–1940) relevé 3 on the page 100, *lectotypus* in Dengler et al. (2004) page 376

Braun-Blanquet scale with cover and sociability – E_3: *Alnus glutinosa* +.2, *Betula pubescens* +.2, *Picea excelsa* +, *Pinus sylvestris* +; E_2: *Alnus glutinosa* 4.3, *Rhamnus frangula* = *Frangula alnus* 1.2, *Rubus species* +, *Sorbus aucuparia* +; E_1: *Caltha palustris* 2.2, *Carex remota* 1.2, *Hydrocotyle vulgaris* 1.2, *Carex vesicaria* 1.1, *Lysimachia vulgaris* 1.1, *Deschampsia cespitosa* +.2, *Dryopteris palustris* = *Thelypteris palustris* +.2, *Lysimachia nummularia* +.2, *Agrostis alba* = *A. stolonifera* +, *Carex canescens* +, *Cirsium palustre* +, *Crepis paludosa* +, *Dryopteris spinulosa* = *D. carthusiana* +, *Epilobium hirsutum* +, *Lythrum salicaria* +, *Peucedanum palustre* +, *Poa palustris* +, *Ranunculus repens* +, *Rumex obtusifolius* +, *Scutellaria galericulata* +, *Solanum dulcamara* +, *Urtica dioica* +, *Valeriana dioica* +; E_0: *Climacium dendroides* +.2, *Mnium punctatum* = *Rhizomnium punctatum* +.2, *Sphagnum cymbifolium* = *S. palustre* +.2, *S. recurvum* +.2

Diagnostic species: *Calamagrostis canescens*, *Calliergon giganteum*, *Calliergonella cuspidata*, *Sphagnum girgensohnii*, *S. squarrosum*

Constant species: ***Alnus glutinosa***, *Betula pubescens* aggr., ***Calamagrostis canescens***, *Calla palustris*, *Calliergon giganteum*, *Calliergonella cuspidata*, *Carex elongata*, *C. lasiocarpa*, *Comarum palustre*, *Dryopteris carthusiana*, ***Frangula alnus***, *Iris pseudacorus*, *Lycopus europaeus*, *Lysimachia thyrsiflora*, ***L. vulgaris***, *Menyanthes trifoliata*, *Peucedanum palustre*, *Phragmites australis*,

Polytrichum commune, ***Salix cinerea***, *Sphagnum palustre* aggr., *Sphagnum squarrosum*, *Thelypteris palustris*

Dominant species: *Alnus glutinosa*, *Calliergon giganteum*, *Carex elongata*, *Phragmites australis*, *Picea abies*, *Salix cinerea*, *Sphagnum palustre* aggr., *S. squarrosum*

Association ***Carici elongatae-Alnetum glutinosae*** **Schwickerath 1933**

Name giving taxa: *Alnus glutinosa* (Linnaeus) Gaertner 1790, *Carex elongata* Linnaeus 1753

Original form of the name (Schwickerath 1933)**:** "*Cariceto elongatae-Alnetum glutinosae*" (p. 116)

Nomenclatural type: Schwickerath (1933) relevé on the page 117, *holotypus*

Braun-Blanquet scale with cover and sociability – E_3: *Alnus glutinosa* 4.4; E_2: *Euonymus europaeus* +.1, *Ribes nigrum* +.1, *Viburnum opulus* +.1; E_1: *Cardamine amara* 3.3, *Caltha palustris* 2.2, *Spiraea ulmaria* = *Filipendula ulmaria* 2.2, *Ranunculus repens* 1.2, *Solanum dulcamara* 1.1, *Aira cespitosa* = *Deschampsia cespitosa* +.2, *Ajuga reptans* +.2, *Angelica sylvestris* +.2, *Glechoma hederacea* +.2, *Scirpus sylvaticus* +.2, *Cardamine pratensis* +.1, *Cardamine sylvatica* = *C. flexuosa* +.1, *Carex acutiformis* +.1, *Carex elongata* +.1, *Carex pallescens* +.1, *Carex paniculata* +.1, *Carex remota* +.1, *Chrysosplenium alternifolium* +.1, *Cirsium palustre* +.1, *Crepis paludosa* +.1, *Equisetum sylvaticum* +.1, *Eupatorium cannabinum* +.1, *Humulus lupulus* +.1, *Lysimachia vulgaris* +.1, *Mentha aquatica* +.1, *Myosotis palustris* = *M. scorpioides* +.1, *Scutellaria galericulata* +.1, *Urtica dioica* +.1, *Valeriana dioica* +.1, *Valeriana officinalis* +.1, E_0: *Acrocladium cuspidatum* = *Calliergonella cuspidata*, *Amblistegium filicinum* = *Cratoneuron filicinum*, *Mnium hornum*

Diagnostic species: *Caltha palustris*, ***Carex elongata***, *Dryopteris carthusiana*, *Filipendula ulmaria*, *Galium palustre*, *Geum rivale*, *Humulus lupulus*, *Iris pseudacorus*, *Lycopus europaeus*, *Plagiomnium affine* aggr., *Ribes nigrum*, *Rubus idaeus*, *Scutellaria galericulata*, *Solanum dulcamara*, *Stachys palustris*, *Thelypteris palustris*

Constant species: ***Alnus glutinosa***, *Athyrium filix-femina*, *Calla palustris*, *Caltha palustris*, *Carex elongata*, *Comarum palustre*, ***Dryopteris carthusiana***, ***Filipendula ulmaria***, *Frangula alnus*, ***Galium palustre***, *Humulus lupulus*, ***Iris pseudacorus***, ***Lycopus europaeus***, ***Lysimachia vulgaris***, *Lythrum salicaria*, ***Phragmites australis***, *Plagiomnium affine* aggr., *Ribes nigrum*, *Rubus idaeus*, *Salix cinerea*, *Scutellaria galericulata*, ***Solanum dulcamara***, *Stachys palustris*, ***Thelypteris palustris***, ***Urtica dioica*** **aggr.**

Dominant species: *Alnus glutinosa*, *Carex elongata*, *Filipendula ulmaria*, *Phragmites australis*, *Thelypteris palustris*, *Urtica dioica* aggr.

Association ***Carici acutiformis-Alnetum glutinosae*** **Scamoni 1935**

Name giving taxa: *Alnus glutinosa* (Linnaeus) Gaertner 1790, *Carex acutiformis* Ehrhart 1789

Original form of the name (Scamoni 1935)**:** "*Alnus glutinosa-Carex acutiformis*-Assoziation" (p. 573)

Nomenclatural type: Mikyška (1968) table I on the page 14, relevé 8, *neotypus* in Neuhäuslová (2003) page 52

Braun-Blanquet scale – E_3: *Alnus glutinosa* 2; E_2: *Alnus glutinosa* 1; E_1: *Carex acutiformis* 5, *Caltha palustris* subsp. *eupalustris* = *C. palustris* 2, *Iris pseudacorus* 2, *Solanum dulcamara* 2, *Carex rostrata* 1, *Cirsium oleraceum* 1, *Equisetum arvense* 1, *Lycopus europaeus* 1, *Lysimachia vulgaris* 1, *Lythrum salicaria* 1, *Cardamine amara* +, *Carex elongata* +, *Crepis paludosa* +, *Filipendula ulmaria* subsp. *pentopelata* = *F. ulmaria* +, *Galium palustre* +, *Geranium palustre* +, *Hydrocotyle vulgaris* +, *Juncus inflexus* +, *Peucedanum palustre* +, *Poa trivialis* +, *Scirpus sylvaticus* +, *Scutellaria galericulata* +, *Thalictrum flavum* r; E_0: *Climacium dendroides* 1

Diagnostic species: *Calystegia sepium*, ***Carex acutiformis***, *C. riparia*, *Equisetum fluviatile*, *Eupatorium cannabinum*, *Galium palustre*, *Glechoma hederacea* aggr., *Humulus lupulus*, *Iris pseudacorus*, *Lycopus europaeus*, *Lysimachia nummularia*, *Prunus padus* subsp. *padus*, *Ribes nigrum*, *Sambucus nigra*, *Scutellaria galericulata*, *Sium latifolium*, *Solanum dulcamara*, *Stachys palustris*, *Symphytum officinale*, *Urtica dioica* aggr., *Viburnum opulus*

Constant species: ***Alnus glutinosa***, *Caltha palustris*, *Calystegia sepium*, ***Carex acutiformis***, *C. riparia*, *Dryopteris carthusiana*, *Equisetum fluviatile*, *Filipendula ulmaria*, *Frangula alnus*, ***Galium palustre***, *Humulus lupulus*, ***Iris pseudacorus***, ***Lycopus europaeus***, ***Lysimachia vulgaris***, *Lythrum salicaria*, *Phragmites australis*, *Ribes nigrum*, *Salix cinerea*, *Scutellaria galericulata*, *Sium latifolium*, ***Solanum dulcamara***, *Symphytum officinale*, *Thelypteris palustris*, ***Urtica dioica*** **aggr.**

Dominant species: *Alnus glutinosa*, *Carex acutiformis*, *C. riparia*

Association ***Salici pentandrae-Betuletum pubescentis*** **Soó 1955**

Name giving taxa: *Betula pubescens* Ehrhart 1789, *Salix pentandra* Linnaeus 1753

Original form of the name (Soó 1955): "*Saliceto pentandrae-Betuletum pubescentis*" (p. 315)

Nomenclatural type: Soó (1955) table 12 on the page 315, *holotypus*

Braun-Blanquet scale – E_3: *Betula pubescens* 3–5, *Betula pendula* 2–4, *Populus tremula* 1, *Quercus robur* 1; E_2: *Cornus sanguinea* 1–2, *Crataegus monogyna* 1, *Frangula alnus* 1, *Salix cinerea* 1–4, *S. pentandra* 1–3, *Rhamnus catharticus* 1, *Sambucus nigra* 1, *Viburnum opulus* – 1; E_1: *Calamagrostis canescens* 4, *Lastrea thelypteris* = *Thelypteris palustris* 2–5, *Carex vesicaria* 2–3, *Geranium palustre* 2, *Agrostis alba* = *A. stolonifera* 1–2, *Alisma plantago-aquatica* 1–2, *Caltha palustris* 1–2, *Carex pseudocyperus* 1–2, *Equisetum palustre* 1–2, *Filipendula ulmaria* 1–2, *Galium palustre* 1–2, *Peucedanum palustre* 1–2, *Urtica dioica* 1–2, *Valeriana officinalis* 1–2, *Angelica palustris* 1, *Angelica sylvestris* 1, *Bidens tripartita* 1, *Calystegia sepium* 1,

Carex appropinquata 1, *Carex muricata* 1, *Cirsium canum* 1, *Cirsium rivulare* 1, *Epilobium parviflorum* 1, *Eupatorium cannabinum* 1, *Euphorbia villosa* = *E. illirica* 1, *Geum urbanum* 1, *Humulus lupulus* 1, *Juncus effusus* 1, *Lycopus europaeus* 1, *Lysimachia vulgaris* 1, *Mentha aquatica* (incl. *M. verticillata*) 1, *Ranunculus repens* 1, *Solanum dulcamara* 1, *Stachys palustris* 1, *Polygonum amphibium* = *Persicaria amphibia* 1, *Prunella vulgaris* 1, *Rubus caesius* 1, *Silene flos-cuculi* 1, *Trollius europaeus* 1, *Veronica longifolia* 1,

Diagnostic species: *Agrostis canina*, *Calamagrostis canescens*, *Molinia caerulea*, *Sphagnum recurvum* aggr.

Constant species: ***Betula pubescens* aggr.**, ***Calamagrostis canescens***, *Carex appropinquata*, *C. lasiocarpa*, ***Comarum palustre***, *Dryopteris carthusiana*, *Frangula alnus*, *Lysimachia thyrsiflora*, ***L. vulgaris***, *Menyanthes trifoliata*, *Molinia caerulea*, *Peucedanum palustre*, *Phragmites australis*, ***Pinus sylvestris***, *Salix cinerea*, *Sphagnum palustre* aggr., *Sphagnum recurvum* aggr., *Thelypteris palustris*

Dominant species: *Betula pubescens* aggr., *Calamagrostis canescens*, *Calliergonella cuspidata*, *Carex appropinquata*, *C. lasiocarpa*, *Sphagnum recurvum* aggr.

S. fallax 1, *Dicranum undulatum* +, *Marchantia polymorpha* +, *Mnium affine* = *Plagiomnium affine* +, *Pleurozium schreberi* +, *Polytrichum strictum* +, *Sphagnum nemoreum* = *S. capillifolium* +

Diagnostic species: *Andromeda polifolia*, ***Carex lasiocarpa***, *C. nigra*, *C. rostrata*, *Eriophorum gracile*, *Menyanthes trifoliata*, *Pinus sylvestris*, *Rhynchospora alba*, ***Sphagnum recurvum* aggr.**, ***Vaccinium oxycoccos* aggr.**

Constant species: ***Andromeda polifolia***, ***Betula pubescens* aggr.**, *Calamagrostis canescens*, ***Carex lasiocarpa***, *C. rostrata*, ***Comarum palustre***, *Frangula alnus*, *Lysimachia thyrsiflora*, ***L. vulgaris***, ***Menyanthes trifoliata***, *Peucedanum palustre*, ***Phragmites australis***, ***Pinus sylvestris***, *Pleurozium schreberi*, *Polytrichum commune*, *P. strictum*, *Rhododendron tomentosum*, *Salix cinerea*, *Sphagnum magellanicum*, *S. palustre* aggr., ***S. recurvum* aggr.**, ***Vaccinium oxycoccos* aggr.**

Dominant species: *Betula pubescens* aggr., *Carex lasiocarpa*, *Menyanthes trifoliata*, *Phragmites australis*, *Pinus sylvestris*, *Sphagnum recurvum* aggr., *Vaccinium oxycoccos* aggr.

Association ***Thelypterido palustris-Betuletum pubescentis* Czerwiński 1972**

Name giving taxa: *Betula pubescens* Ehrhart 1789, *Thelypteris palustris* Schott 1834

Original form of the name (Czerwiński 1972)**:** "*Dryopteri thelypteris-Betuletum pubescentis*" (p. 121)

Nomenclatural type: Czerwiński (1972) table 7 on the page 135, relevé 3, *lectotypus* hoc loco, Braun-Blanquet scale – E_3: *Betula pubescens* (a) 3, *Picea excelsa* (a) 1, *Pinus sylvestris* (a) 1; E_2: *Frangula alnus* (b) 3, *Picea excelsa* (b) 2, *Sorbus aucuparia* (b) 1, *Betula pubescens* (b) 1, *Juniperus communis* (b) +, *Salix cinerea* (b) +; *Acer pseudoplatanus* (c) +, *Frangula alnus* (c) +, *Quercus robur* (c) +, *Sorbus aucuparia* (c) +; E_1: *Carex lasiocarpa* 2, *Dryopteris thelypteris* = *Thelypteris palustris* 2, *Vaccinium myrtillus* 2, *Calamagrostis canescens* 1, *Cirsium palustre* 1, *Comarum palustre* 1, *Dryopteris spinulosa* = *D. carthusiana* 1, *Galium palustre* 1, *Lysimachia vulgaris* 1, *Maianthemum bifolium* 1, *Menyanthes trifoliata* 1, *Myosotis palustris* = *M. scorpioides* 1, *Phragmites australis* 1, *Vaccinium vitis-idaea* 1, *Viola palustris* 1, *Agrostis canina* +, *Caltha palustris* +, *Carex elongata* +, *C. pseudocyperus* +, *Dryopteris cristata* +, *Geum rivale* +, *Luzula pilosa* +, *Oxycoccus quadripetalus* = *Vaccinium oxycoccus* +, *Paris quadrifolia* +, *Peucedanum palustre* +, *Pyrola rotundifolia* +, *Pyrola secunda* = *Orthilia secunda* +, *Ranunculus repens* +, *Urtica dioica* +, *Vaccinium uliginosum* +; E_0: *Sphagnum palustre* 2, *Climacium dendroides* 1, *Eurhynchium zetterstaedtii* = *E. angustirete* 1, *Rhytidiadelphus triquetrus* 1, *Sphagnum apiculatum* =

Association ***Eriophoro vaginati-Betuletum pubescentis* (Hueck 1929) Passarge et Hofmann 1968**

Name giving taxa: *Betula pubescens* Ehrhart 1789, *Eriophorum vaginatum* Linnaeus 1753

Original form of the name (Hueck 1929)**:** "*Betula pubescens-Eriophorum vaginatum-Sphagnum recurvum*–Ass." (p. 129)

Nomenclatural type: Hueck (1929) table 32 on the page 132, relevé 4, *lectotypus* in Hrivnák et al. (2021) page 43

Braun-Blanquet scale –E_3: *Betula pubescens* 3; E_1: *Eriophorum vaginatum* 4, *Vaccinium oxycoccos* 1, *Aspidium spinulosum* = *Dryopteris carthusiana* +, *Betula* sp. +, *Vaccinium myrtillus* +; E_0: *Sphagnum recurvum* 5, *Sphagnum medium* 1, *Aulacomnuim paluste* +

Diagnostic species: *Andromeda polifolia*, *Calluna vulgaris*, ***Eriophorum vaginatum***, *Pinus sylvestris*, *Polytrichum strictum*, ***Rhododendron tomentosum***, *Sphagnum magellanicum*, *S. recurvum* aggr., ***Vaccinium oxycoccos* aggr.**, *V. uliginosum*

Constant species: ***Andromeda polifolia***, ***Betula pubescens* aggr.**, ***Carex lasiocarpa***, ***Eriophorum vaginatum***, ***Pinus sylvestris***, *Pleurozium schreberi*, ***Polytrichum strictum***, ***Rhododendron tomentosum***, *Sphagnum magellanicum*, ***S. recurvum* aggr.**, ***Vaccinium oxycoccos* aggr.**

Dominant species: *Betula pubescens* aggr., *Eriophorum vaginatum*, *Pinus sylvestris*, *Polytrichum strictum*, *Rhododendron tomentosum*, *Sphagnum magellanicum*, *Sphagnum recurvum* aggr., *Vaccinium oxycoccos* aggr.

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Supplementary material

Supplementary material 1
Data sources of vegetation plots used for the analysis (pdf. file)
Link: https://doi.org/10.3897/VCS.122617.suppl1

Supplementary material 2
List of species and subspecies merged to aggregates (aggr.) (pdf. file)
Link: https://doi.org/10.3897/VCS.122617.suppl2

Supplementary material 3
Results of unsupervised classification of vegetation plots dominated by *Alnus glutinosa* and *Betula pubescens* (pdf. file)
Link: https://doi.org/10.3897/VCS.122617.suppl3

Supplementary material 4
Full synoptic table of the class *Alnetea glutinosae* in Ukraine (csv. file)
Link: https://doi.org/10.3897/VCS.122617.suppl4

Supplementary material 5
List of associations of alder carr and birch swamps reported from Ukraine (pdf. file)
Link: https://doi.org/10.3897/VCS.122617.suppl5